

Molecular phylogeny, morphology and bioacoustics reveal five additional species of arboreal microhylid frogs of the genus *Anodonthyla* from Madagascar

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Abstract

We provide a partial revision of the microhylid frogs of the genus *Anodonthyla*, endemic to Madagascar, based on comprehensive molecular, bioacoustic and morphological data sets that include newly collected specimens from multiple localities. The molecular trees provide strong evidence for the polyphyly of several nominal species as they were previously defined, especially of *Anodonthyla boulengeri* and *A. nigrigularis*. As a consequence, we here resurrect the nomen *Mantella pollicaris* Boettger as *Anodonthyla pollicaris* from the synonymy of *A. boulengeri*, and we describe four new species, all with strong genetic divergences to other nominal species: *Anodonthyla emilei* from Ranomafana National Park, a comparatively medium-sized species characterized by a multi-note advertisement call with high note repetition rate; *A. theoi* from Manombo Special Reserve, a small species characterized by low note repetition rate, long note duration and high spectral call frequency; *A. vallani*, a medium-sized species from Ambohitantely Special Reserve, characterized by low note repetition rate, long note duration and low spectral call frequency; and *A. jeanbai*, a small species from Andohahela National Park, characterized by a long and narrow head, presence of short dorsolateral folds, a very short first finger, and a yellowish ventral colour. A further candidate species comprises populations previously assigned to *A. boulengeri* from the Ranomafana region, which we do not describe because the corresponding data set is too fragmentary, and we refer to it as *A. sp. aff. boulengeri* ‘Ranomafana’. The molecular phylogeny indicates recurrent shifts between high and low note repetition rates in calls, based mainly on three strongly supported sister groups: *A. moramora* with low repetition rate and *A. nigrigularis* with moderately low repetition rate; *A. theoi* with low repetition rate and *A. pollicaris* with high repetition rate; and *A. vallani* with low repetition rate and *A. sp. aff. boulengeri* ‘Ranomafana’ with high repetition rate. The two species with the northernmost ranges, *A. hutchisoni* and *A. boulengeri*, are phylogenetically nested within clades of species occurring further south, confirming that the center of origin of the genus *Anodonthyla* was most likely in the South East of Madagascar.

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Introduction

Frogs of the family Microhylidae Günther, 1859 are among the most poorly known amphibian groups. Several factors contribute to the difficulty of their study: some species have a very seasonal breeding behaviour and are thus difficult to find, other species are minute in body size and therefore often overlooked. The high frequency of evolutionary change in some osteological characters, especially reductions in the shoulder girdle, has led to the definition of a large number of microhylid genera containing only one or a few species, and phylogenetic relationships among genera and among major microhylid clades have long remained enigmatic. Recently, molecular data have started to decipher microhylid diversity and relationships. Studies of multigene datasets have produced

the first comprehensive phylogenies of major microhylid lineages (Van der Meijden *et al.*, 2004, 2007; Van Bocxlaer *et al.*, 2006) although several basal relationships remained unclarified. Phylogenies based on dense taxon sampling of microhylids from New Guinea (Köhler and Günther, 2008) and Madagascar (Andreone *et al.*, 2005b; Wollenberg *et al.*, 2008) provided evidence for a high proportion of undescribed diversity, with many candidate species exhibiting high genetic divergence to all known species.

In Madagascar, microhylids are represented by three subfamilies: the Dyscophinae Boulenger, 1882 with one genus and three species, the Scaphiophryinae Laurent, 1946 with two genera and ten species, and the Cophylinae Cope, 1889 with seven genera and 45 species (Glaw and Vences, 2007; Fenolio *et al.*, 2007). Molecular data indicate that scaphiophrynines and cophylines together form a clade that is endemic to Madagascar and has unclarified relationships to other microhylids, whereas dyscophines form a separate evolutionary lineage related to Asian microhylids (Van der Meijden *et al.*, 2007). Although new species of scaphiophrynines have been discovered in the last years (*e.g.* Glos *et al.*, 2005; Andreone *et al.*, 2006), the bulk of undescribed microhylid diversity in Madagascar is found in the Cophylinae (Wollenberg *et al.*, 2008; Vieites *et al.*, 2009).

Cophylines are characterized by a derived mode of larval development: whereas most microhylids have a specialized filter-feeding tadpole, cophylines have non-feeding tadpoles that develop either in tree holes, terrestrial foam nests, or terrestrial jelly nests (Blommers-Schlösser, 1975; Glaw and Vences, 2007; Grosjean *et al.*, 2007). Most cophylines have very simple advertisement calls, consisting of single melodious notes that are repeated after regular intervals and for long periods of time, usually lasting several minutes. Correlated to the reproductive mode of the various cophyline lineages is their arboreal versus terrestrial or fossorial ecology, and apparently, multiple evolutionary shifts between arboreal and terrestrial habits have occurred in this subfamily (Andreone *et al.*, 2005b).

One of the arboreal lineages in the Cophylinae is the genus *Anodonthyla* Müller, 1892 which is a well-defined monophyletic group based on both molecular and morphological characters (Blommers-Schlösser and Blanc, 1991; Andreone *et al.*, 2005b; Aprea *et al.*, 2007; Wollenberg *et al.*, 2008). One of the most obvious morphological synapomorphies of the genus is the presence, in males only, of a large prepollex that

runs along the first finger and generally is closely connected to the first finger over most of its length. Correlated to this character, in males and females, the first finger is very short compared to other cophylines.

Anodonthyla at present comprises six species (Blommers-Schlösser, 1975; Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 2005, 2007; Fenolio *et al.*, 2007), of which five are arboreal species that breed, as far as known, in holes of tree or bamboo trunks: *Anodonthyla boulengeri* Müller, 1892; *A. hutchisoni* Fenolio, Walvoord, Stout, Randrianirina, and Andreone, 2007; *A. moramora* Glaw and Vences, 2005; *A. nigrigularis* Glaw and Vences, 1992; *A. rouxae* Guibé, 1974. In contrast, *Anodonthyla montana* Angel, 1925 appears to be restricted to areas of the granitic Andringitra massif above the tree line and here breeds in small rock cavities. However, preliminary data already indicated that these species numbers are underestimations since the available molecular and bioacoustic evidence pointed to several highly divergent genealogical lineages within *A. boulengeri*, and to geographically highly distant populations within *A. nigrigularis* that warranted further taxonomic study (Vallan, 2000; Glaw and Vences, 2005, 2007; Fenolio *et al.*, 2007). Here we present a survey of molecular variation based on mitochondrial genes, in combination with bioacoustic and morphological data from new *Anodonthyla* collections mainly obtained through intensive fieldwork over the past five years. Based on these data we conduct a partial revision of the genus that leads to the description of four new species and the resurrection of one further species from synonymy.

Material and methods

Specimens were collected at night by opportunistic searching and localizing calling males, using torches and head lamps. They were euthanized in a chlorobutanol solution, fixed in 95% ethanol or 7% formalin, and preserved in 70% ethanol. Locality information was recorded with GPS receivers. Specimens studied in this paper are deposited in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN), Naturhistorisches Museum Basel (NMBA), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF), Université d'Antananarivo, Département de Biologie Animale, Antananarivo (UAD-BA), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Zoologisch Museum Amsterdam (ZMA), and the Zoologische Staatssammlung

München (ZSM). FGMV, FGZC and ZCMV refer to F. Glaw and M. Vences field numbers, respectively; FAZC refers to F. Andreone field numbers. MRSN is used as acronym for the Museo Regionale di Scienze Naturali di Torino. Terminology for biogeographic regions of Madagascar follows Boumans *et al.* (2007) (see also Glaw and Vences, 2007).

Morphology. Morphological measurements (in millimetres) were all taken by M. Vences with digital calipers (precision 0.01 mm) to the nearest 0.1 mm. Used abbreviations are: SVL (snout-vent length), HW (greatest head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), PREP (prepollex length), TL (tibia length), HAL (hand length), HIL (hindlimb length), FL (foot length), FOTL (foot length including tarsus), FORL (forelimb length), and RHL (relative hindlimb length). Terminology and description scheme follow Glaw and Vences (2005) and Glaw and Vences (1997) for eye colouration. Morphological differentiation was analyzed by computing residuals of all morphological variables except TD (for which data are incomplete) to SVL, and the obtained residuals were submitted to a Principal Component Analysis (PCA) in STATISTICA (StatSoft, Tulsa, Oklahoma, USA). We then plotted values of the Principal Component with highest Eigenvalue against SVL, and the ratio of the residuals of HW and HL to infer morphological differentiation among *Anodonthyla* species.

Bioacoustics. Calls were recorded in the field using different types of tape recorders (Sony WM-D6C, Tensai RCR-3222) and external microphones (Sennheiser Me-80, Vivanco EM 238), or with an Edirol R-09 24-bit digital recorder with internal microphone and saved as uncompressed files. Recordings were sampled (or re-sampled) at 22.05 kHz and 16-bit resolution and computer-analysed using the software CoolEdit98. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points). Spectrograms were obtained at Hanning window function with 256 bands resolution. Temporal measurements are given as range, with mean \pm standard deviation in parentheses. Terminology in call descriptions follows Köhler *et al.* (2005a).

Molecular phylogeny. In order to provide information on the genetic homogeneity of species and their phylogeny, we assembled two molecular data sets. (1) For DNA barcoding purposes, we sequenced for a data set of 63 *Anodonthyla* specimens a fragment of

the mitochondrial 16S rRNA gene, using primers 16SL3 and 16SAH as in Vences *et al.* (2003). The final alignment contained 500 nucleotide positions. We computed a Bayesian inference tree using MrBayes V.3.1.2. (Ronquist and Huelsenbeck, 2003) and a Maximum Likelihood bootstrap tree using the RaxML server (Stamatakis *et al.* 2008), following detailed protocols for selection of substitution models as described below. (2) To reliably assess the phylogenetic relationships among *Anodonthyla* species, we compiled a multi-gene dataset comprising one specimen for all nominal species and for most of the previously identified genetically divergent lineages of *Anodonthyla*. A dataset of 16S and 12S rRNA and cytochrome *b* gene sequences for most of these was available from Wollenberg *et al.* (2008). We complemented this data set for a number of additional individuals using primers and protocols as in Vences *et al.* (2003) and Wollenberg *et al.* (2008), and added partial sequences of the cytochrome oxidase subunit I using standard barcoding protocols and primers (Hebert *et al.*, 2003). Altogether we assembled a concatenated dataset of 3187 basepairs, being comprised of 700 basepairs of the mitochondrial 12S rRNA gene, of two fragments of the 16S rRNA gene (539 and 737 bp, respectively), and of each a fragment of the mitochondrial cytochrome *b* (cob, 574 bp) and cytochrome oxidase subunit I (cox1, 637 bp) genes (for Genbank accession numbers of most sequences see Wollenberg *et al.*, 2008; accession numbers are GU048760-GU048808 and GU177051-GU177078 for newly determined sequences). A sequence of the dyscophine species *Dyscophus antongilii* was added as outgroup taxon, and the cophyline species *Platyplelis grandis* and *Stumpffia gimmeli* were added to the dataset to obtain hierarchical outgroups. Congruence of single-gene phylogenetic topologies was verified by comparing Neighbor-joining trees before computing a phylogeny from the concatenated dataset. For the concatenated dataset, the best-fit model of evolution was inferred using the FINDMODEL online interface of the HIV database (accessible via <http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>).

Phylogenies were constructed using Bayesian inference (using MrBayes V.3.1.2., Ronquist and Huelsenbeck, 2003, with 3.2 million generations), Maximum Likelihood using the online interface of PhyML (Guindon and Gascuel, 2003), and Maximum Parsimony using PAUP* (V. 4.0.b10, Swofford, 2002), with 2000 (ML) and 1000 (MP) bootstrap replicates.

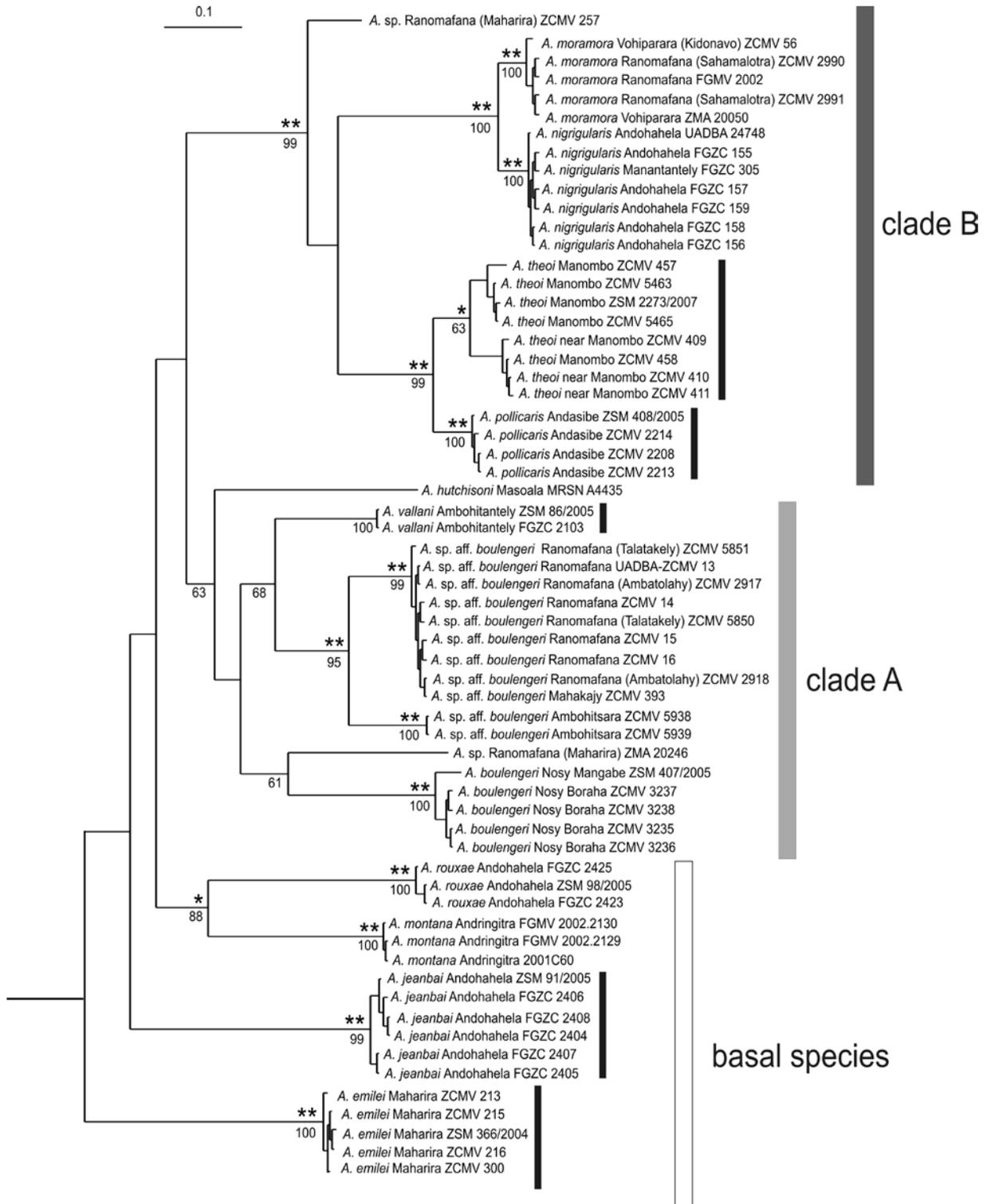


Fig. 1. Phylogenetic tree of *Anodonthyla* species based on Bayesian Inference analysis of partial sequences of the 16S rRNA gene (500 bp). *Dyscophus antongilii* (Dyscophinae) was used as outgroup. Black bars mark species newly described or revalidated in the present paper (Appendix). Asterisks and numbers show nodal support from Bayesian posterior probabilities (* ≥ 0.95 , ** ≥ 0.99), and Maximum Likelihood bootstrap analysis (not shown if posterior probability < 0.95 or bootstrap values < 50).

Results

Molecular diversity and phylogenetic relationships of *Anodonthyla*

The tree based on 16S sequences as reproduced in Fig. 1 reveals the presence of numerous deep genealogical lineages within *Anodonthyla*. Most of the populations studied were strongly differentiated but specimens from the same populations were genetically very similar or had identical haplotypes. The tree based on concatenated sequences of four mitochondrial genes (Fig. 2) corroborates most of the phylogenetic relationships suggested by the 16S rRNA tree and provides a better phylogenetic resolution, although several basal relationships remain unresolved. Exploratory separate analyses of each of the gene fragments yielded concordant results (not shown).

The results support the monophyly of the genus *Anodonthyla* (Fig. 2) and clearly define genetically all nominal species of the genus although a redefinition of two of these, *A. boulengeri* and *A. nigrigularis*, becomes necessary.

In the following we review the identity of the various genetically homogeneous clades as identified in

Fig. 1 and their phylogenetic relationships as recovered by the combined analysis (Fig. 2).

According to the multi-gene analysis (Fig. 2) two well-defined and described species occurring in high-elevation habitats of south-eastern Madagascar, *A. montana* and *A. rouxae*, form a monophyletic group and are placed in a basal position in *Anodonthyla*. The next most basal clade (but placed as most basal clade in Fig. 1) is made up by a large species from various localities in Ranomafana National Park which has a unique advertisement call and is described herein as *Anodonthyla emilei* (Appendix).

A second strongly divergent species that occupies a basal position in both trees (Figs 1-2) is made up by small-sized specimens from high elevations in Andohahela National Park in south-eastern Madagascar. These specimens show subtle but constant differences to other *Anodonthyla* in morphology and colouration (see below) and are herein described as *A. jeanbai* (Appendix).

The remaining *Anodonthyla* are grouped in two major clades. The first of these (here named clade A) contains specimens that we assign to *A. boulengeri* (from the central east coast of Madagascar: Nosy Boraha and Nosy Mangabe) as well as *A. hutchisoni*. The

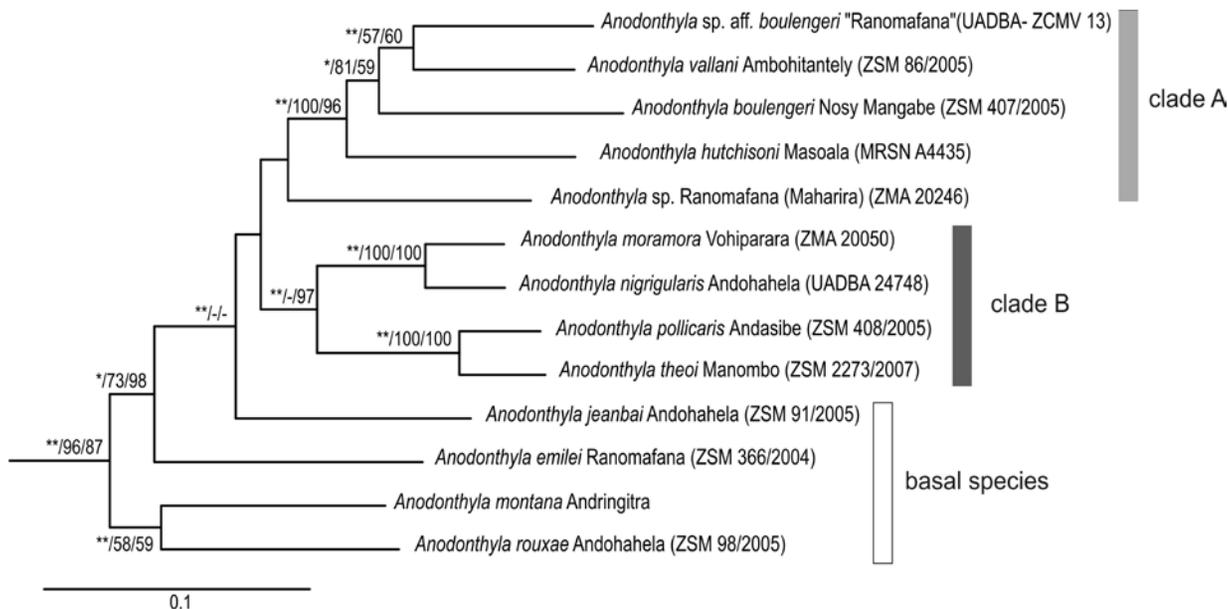


Fig. 2. Phylogenetic tree of *Anodonthyla* species based on Bayesian Inference analysis of the concatenated sequences of 12S rRNA, 16S rRNA, cytochrome *b* and cytochrome oxidase subunit I sequences (3187 bp). *Dyscophus antongilii* (Dyscophinae) was used as outgroup, *Stumpffia gimmeli* and *Platypelis grandis* (Cophylinae) were included as hierarchical outgroups (not shown). Asterisks and numbers show nodal support from Bayesian posterior probabilities (≥ 0.95 , ≥ 0.99), and Maximum Likelihood and Maximum Parsimony bootstrap analysis (not shown if posterior probability < 0.95 or bootstrap values < 50).

populations of *A. boulengeri* (also including one specimen from Foulpointe, not shown in Fig. 1) have a pairwise 16S divergence of 1.1–1.6%. Furthermore, this clade contains several deeply differentiated genealogical lineages: (1) Specimens from Ambohitantely which in morphology and advertisement calls are closer to *A. nigrigularis* than to *A. boulengeri*; these are herein described as *A. vallani* (Appendix). (2) Specimens from the Ranomafana area (Ranomafana, Mahakajy, Ambohitsara) that by morphology and advertisement call superficially resemble *A. boulengeri*, although small but constant bioacoustic differences are evident. Interestingly, specimens from the locality Ambohitsara show a pronounced genetic divergence to those from Ranomafana and Mahakajy. We refer to these specimens here as *A. sp. aff. boulengeri* ‘Ranomafana’ and refrain from a formal species de-

scription until more in-depth analyses on these populations become available (Appendix). (3) One specimen (ZMA 20246) is genetically distinct and probably represents a further undescribed species from the Ranomafana area, but no further data are available for this individual.

The second major clade within *Anodonthyla* (clade B) contains specimens of *A. nigrigularis* and *A. moramora* which are sister species with high support. These two species have a relatively low genetic divergence of 2.0% in the 16S rRNA gene. Furthermore this clade contains (1) specimens from Andasibe that previously were considered to be *A. boulengeri* but are placed sister to (2) a species from Manombo in the south-east that distinctly differs from other *Anodonthyla* in advertisement calls. We here resurrect the name *A. pollicaris* for the Andasibe population and

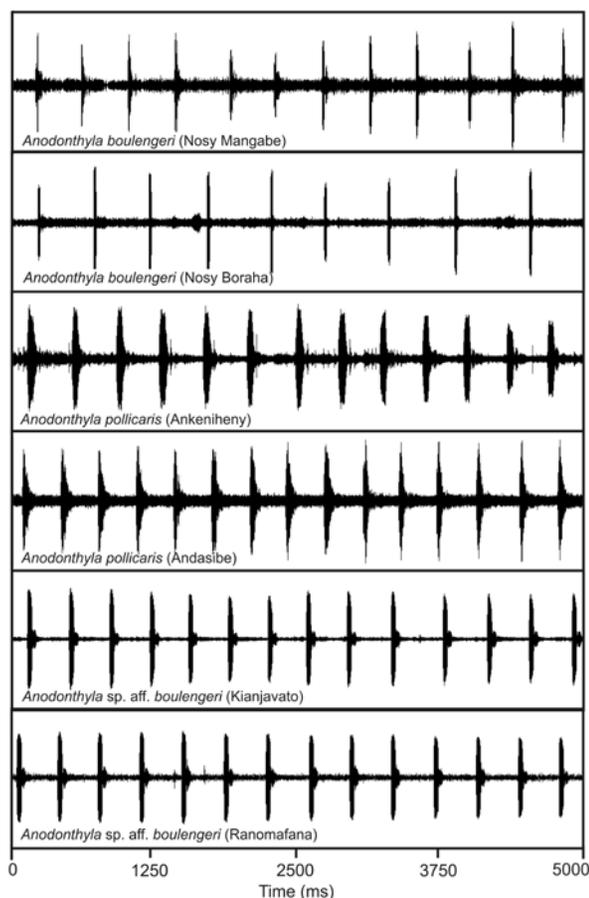


Fig. 3. Comparative waveforms of parts of call series of *Anodonthyla boulengeri*, *A. pollicaris*, and *A. sp. aff. boulengeri* ‘Ranomafana’ at same time scale. For details of localities and recording dates, see Table 3.

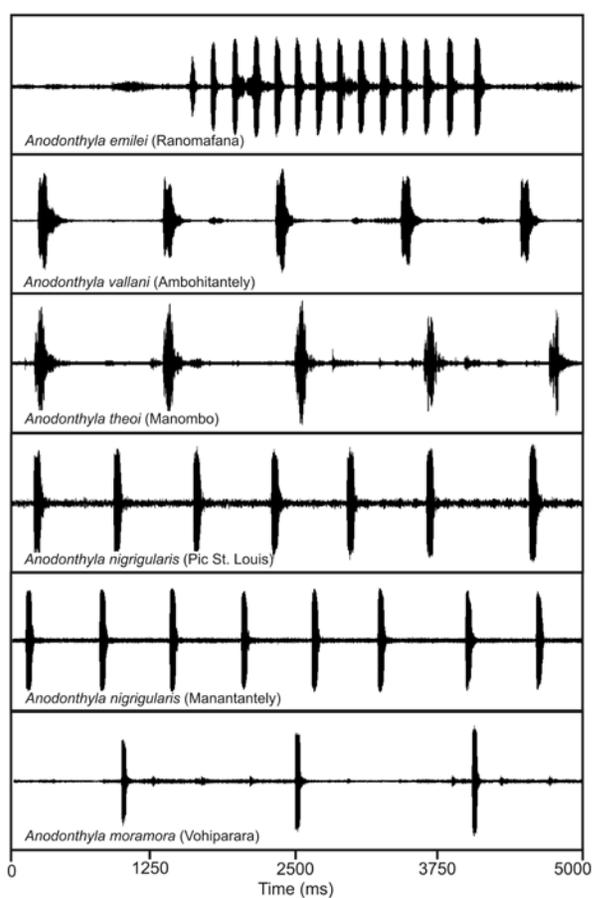


Fig. 4. Comparative waveforms of parts of call series of *Anodonthyla emilei*, *A. vallani*, *A. theoi*, *A. nigrigularis*, and *A. moramora* at same time scale. For details of localities and recording dates, see Table 3.

describe the Manombo population as a new species, *A. theoi* (16S divergence between these two species: 3.5%; Appendix). Finally, this clade contains (3) a further isolated specimen from the Ranomafana area (ZCMV 257) that probably represents an undescribed species but for which no further data are available.

Bioacoustic and morphological differentiation of Anodonthyla species

The molecular data (Figs 1-2) indicate that several species as previously understood (*e.g.* Glaw and Vences, 1994) in fact probably represent complexes of various species. Because our molecular data set includes only mitochondrial genes we cannot use the criterion of congruence of various unlinked loci (*i.e.*, following the genealogical concordance method of phylogenetic species recognition, GCPSR; Avise and Ball, 1990) to define species of *Anodonthyla* and need to take into account the possibility that some of the unexpected phylogenetic relationships may be due to introgression.

However, a detailed comparison of bioacoustic and morphological data indicates that in almost all cases the mitochondrial lineages identified are congruent with these independent taxonomic characters.

Advertisement calls, as represented by oscillograms in Figs 3-4 and described in detail in the Appendix, allow to easily separate various forms discovered by the molecular analysis, and to corroborate their status as distinct species. *Anodonthyla emilei* has a unique call consisting of a rapid note series rather than regularly repeated single notes. Calls of *A. vallani* and *A. theoi* differ by their slow note repetition rate, with values intermediate those of *A. nigrigularis* and *A. moramora*, from all other species; and calls of *A. theoi* can be distinguished by a distinctly higher spectral frequency from those of *A. vallani* (Appendix). Furthermore, among the species with rapid note repetition rate, it is possible to distinguish *A. boulengeri* by its very short note duration from *A. pollicaris*; although subtle, this difference is constant across localities and easily measurable. Hence, except for *A. jeanbai* whose calls are unknown, all species newly described or revalidated herein have a bioacoustic differentiation concordant with their molecular differentiation.

Morphological data yielded a number of additional taxonomic characters to differentiate some of the newly discovered species. Most importantly, *A. jeanbai* for which bioacoustic data are lacking can be recognized



Fig. 5. Views of palmar surfaces of males of various *Anodonthyla* species, showing relative size and degree of separation of first finger and prepollex. Not to scale.

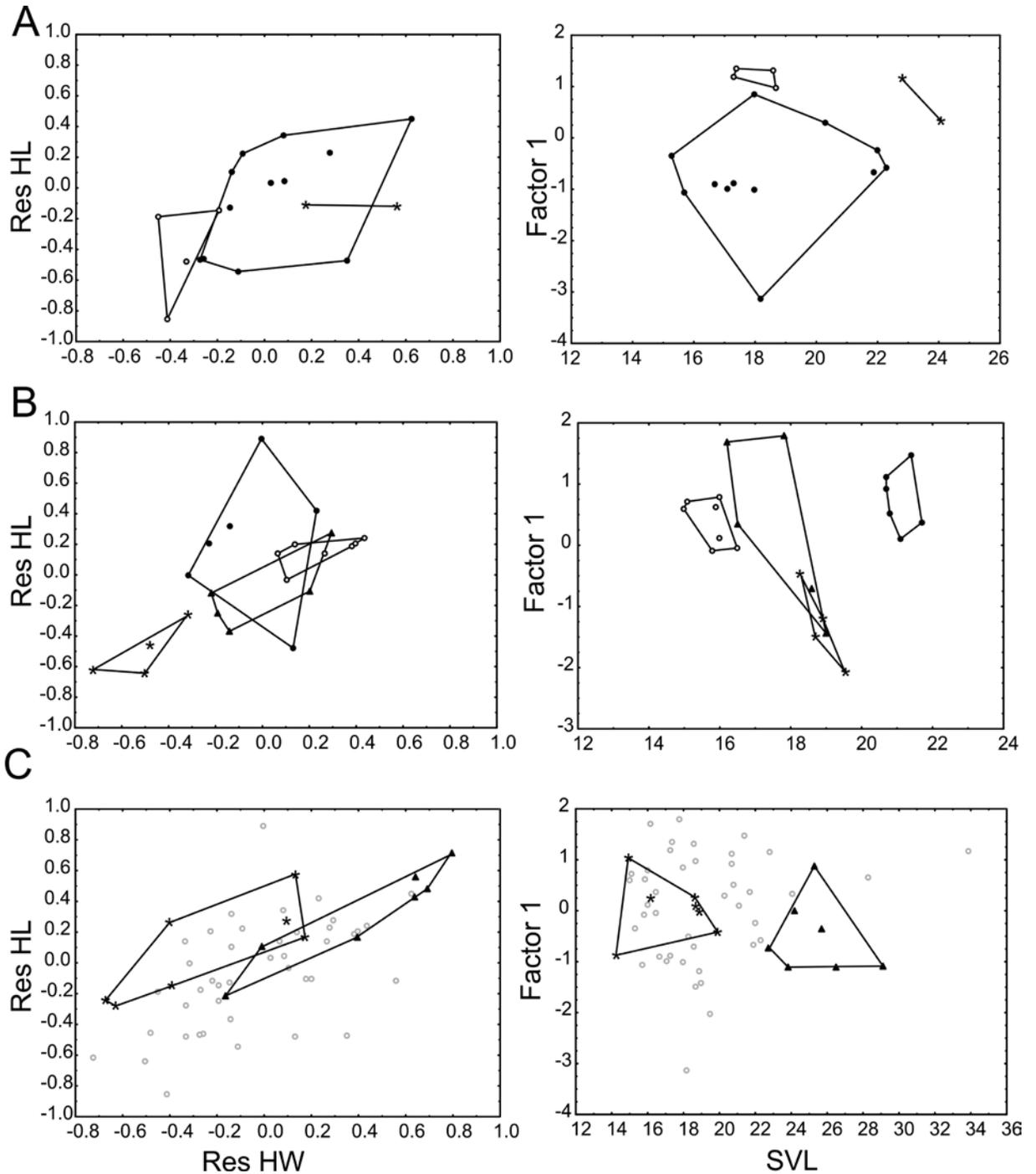


Fig. 6. Morphometric differentiation of the nine species with respect to their phylogenetic position (data see Table 2). A – *A. vallani* (asterisks), *A. boulengeri* (filled dots), *A. sp. aff. boulengeri* 'Ranomafana' (empty dots). B – *A. theoi* (asterisks), *A. pollicaris* (triangles), *A. nigrigularis* (filled dots), *A. moramora* (empty dots). C – *A. jeanbai* (asterisks), *A. emilei* (triangles), all other specimens (empty circles).

by a yellowish ventral side (only shared with *A. moramora*), presence of a short tubercular dorsolateral fold posterior to the eye, and an extremely short first finger (shorter than prepolex; Fig. 5). *A. emilei* differs from most other species by its large size in combination with a rather tubercular dorsal skin. For further diagnostic characters, see Appendix.

Morphometric data can further be used to distinguish several of those species that by the molecular data are placed phylogenetically close to each other. The PCA of the residuals of the morphological variables yielded four factors with Eigenvalues <1 in Varimax-raw rotated coordinate system (explaining 33%, 16.9%, 9.9%, and 7.8% of total variance, respectively). The factor with highest Eigenvalue received high factor loadings from the variables HIL, FOTL, FL, TIBL and RHL and was found to be useful in differentiating *Anodonthyla* species together with SVL, as well as the ratio of the residuals of HW and HL (ResHW/ResHL) (Fig. 6). In the molecular clade containing *A. sp. aff. bouleengeri* ‘Ranomafana’ as sister to *A. vallani* and *A. bouleengeri* all three species can be well distinguished according to both their factor1/SVL and ResHW/ResHL ratios (Fig. 6a). In the well-supported clade containing the two sister species pairs *A. pollicaris* and *A. theoi*, and *A. moramora* and *A. nigrigularis*, the latter pair can be distinguished by their factor1/SVL ratio. Although *A. pollicaris* and *A. theoi* have overlapping factor1/SVL ratios, their ResHW/ResHL ratios are non-overlapping (Fig. 6b). The phylogenetic placement of the other two newly described *Anodonthyla* species, *A. jeanbai* and *A. emilei*, is not well resolved. Although their ResHW/ResHL ratios are overlapping, they can be morphologically well distinguished with their factor1/SVL ratio (Fig. 6c). No clear distinction was possible between *A. bouleengeri* and *A. pollicaris* by morphometry (not shown), largely due to the high variability of *A. bouleengeri* and relatively low sample sizes for both species.

Summarizing, there are concordant arguments from the molecular, bioacoustic and/or morphological data to accept five additional species in the genus *Anodonthyla* (*A. emilei*, *A. jeanbai*, *A. pollicaris*, *A. theoi*, *A. vallani*, besides the previously known *A. bouleengeri*, *A. hutchisoni*, *A. nigrigularis*, *A. montana*, *A. moramora*, and *A. rouxae*). A summary of the major diagnostic differences between these species is given in Table 1. Taxonomic accounts and species descriptions are found in the Appendix and illustrated in Figs 7-17. The geographical distribution of all *Anodonthyla* species is summarized in Fig. 18. For three additional deep genealogical lineages our data are insufficient for

a definitive taxonomic conclusion: *Anodonthyla sp. aff. bouleengeri* ‘Ranomafana’ (including a strongly divergent population from Ambohitsara) is morphologically highly similar to *A. bouleengeri* and *A. pollicaris* and the bioacoustic differences to *A. pollicaris* are minor. For this form, further work including independent (nuclear) molecular markers are needed to assess whether indeed it represents an independent evolutionarily lineage. In addition, two enigmatic individuals from Ranomafana clustered far from all other *Anodonthyla* and may represent two additional species, but no bioacoustic or morphological information is available for these individuals which therefore, following the terminology of Vieites *et al.* (2009), should be considered as unconfirmed candidate species.

Discussion

Species diversity in Anodonthyla

Numbers of amphibian species in Madagascar have recently experienced a steep increase (Köhler *et al.*, 2005b; Vieites *et al.*, 2009). This was caused by a number of factors. On one hand, a high intensity of field inventories in areas previously poorly surveyed for amphibians, but also at well-known sites. On the other hand, the stringent application of a combination of different data sets in taxonomic assessments, namely DNA barcoding, bioacoustics, and morphology. The application of DNA barcoding as a first step, with subsequent confirmation of candidate species by bioacoustics and/or morphology, has proven to be the most efficient approach, and Vieites *et al.* (2009) report on 126 undescribed but confirmed candidate species of amphibians from Madagascar. As already remarked by Wollenberg *et al.* (2008), cophylines are among the lineages with the highest proportion of undescribed species diversity, and also the proportion of unconfirmed candidate species (those defined by a high genetic divergence but unstudied for bioacoustics and morphology) is highest.

Our study in *Anodonthyla* shows that the candidate species of at least this cophyline genus are not just deep genealogical lineages, but also show clear bioacoustic and morphological differences upon detailed analysis and thus correspond to well-defined species, of which only a few qualify as true ‘cryptic species’. For example, and besides the rather easily scored morphological differences mentioned in the species diagnoses, there are also more subtle but clear differences

in morphometric variables defining most of the species (e.g. Fig. 6). It is also remarkable that the genetic divergences among species of *Anodonthyla* in general are very high. Low divergences are only observed among *A. moramora* and *A. nigrigularis* (2% divergence in the 16S rRNA gene), and *A. pollicaris* and *A. theoi* (3.5%). In contrast, all other pairwise comparisons yielded divergences of 7.4% or higher, up to 13.7% between *A. vallani* and one unconfirmed candidate species from Maharira (Ranomafana).

This latter unconfirmed candidate species merits some further discussion: in fact, it corresponds to a single sample (ZMA 20246, corresponding to field number ZCMV 204) of a possibly juvenile specimen collected in the leaf litter at Maharira, in syntopy with *A. emilei*. Because the corresponding voucher specimen was not available for our study, no further statements are currently possible, but considering the very high divergence of this sample to all other species of the genus (9.7–13.7%), it is likely that a further undescribed species of *Anodonthyla* occurs at this site. Even more remarkable, a second isolated specimen collected during the same expedition at the same locality (no habitat or bioacoustic data; specimen ZCMV 257) shows, again, a deep divergence to all other species. Considering these two unconfirmed candidate species would bring the number of *Anodonthyla* in Ranomafana National Park up to five (in addition, *A. sp. aff. boulengeri* ‘Ranomafana’, *A. emilei*, and *A. moramora*).

Cophylines, in general are characterized by a relatively fast rate of mitochondrial evolution, at least compared to scaphiophrynines where substitutions appear to accumulate at a very slow pace in the mitochondrial DNA (Vences et al., 2002a). It is nevertheless unlikely that the deep divergences between most species of *Anodonthyla* are caused by a particularly fast mitochondrial substitution rate in this genus. Instead, we assume that most of these are in fact old species, and this hypothesis is supported by the fact that some well differentiated species in *Anodonthyla* show low divergences around or even below the threshold of 3% 16S distance proposed by Fouquet et al. (2007) to delimit candidate species in frogs. One species for which we had samples from more than one population available for genetic analysis (*A. boulengeri sensu stricto*) in fact showed divergences of 1.1–1.6% between populations which also had some important morphological differences. This indicates that our revision has certainly not completed the species inventory of *Anodonthyla*. Besides *A. sp. aff.*

boulengeri ‘Ranomafana’, the two unconfirmed candidate species from Maharira, and possibly the deviant *A. boulengeri* population from Nosy Mangabe, we expect that further inventories, especially in the South East of Madagascar, will yield additional new species of this genus.

Biogeography

According to the previous classification, several species of *Anodonthyla* were relatively widespread. For instance, *A. boulengeri* was recorded from Marojejy to Andohahela along most the eastern escarpment of Madagascar (Blommers-Schlösser and Blanc, 1991), and *A. nigrigularis* from localities in the South East as well as from Ambohitantely at the western edge of the Northern Central East (Vallan, 2000).

Evidence has since progressively accumulated that these wide distributions are artificial and reflect poor taxonomic knowledge. Glaw and Vences (1992) described a new species, *A. nigrigularis*, from the extreme South East of Madagascar, invalidating records of *A. boulengeri* from this area. Vences et al. (2002b) found that the northernmost records from Marojejy in fact do not belong to the genus *Anodonthyla*. Fenolio et al. (2007) found what probably are the northernmost *Anodonthyla* populations and assigned them to a new species, *A. hutchisoni*, probably endemic to Masoala Peninsula. Finally, in the present paper, we demonstrate that the geographically disparate population of *A. nigrigularis* from Ambohitantely in fact represents a distinct species, *A. vallani*, and we partition *A. boulengeri* into three species: *A. boulengeri sensu stricto*, *A. pollicaris*, and *A. sp. aff. boulengeri* ‘Ranomafana’.

As a consequence of this taxonomic progress, and if we disregard an unconfirmed record of *A. montana* from Andohahela (Blommers-Schlösser and Blanc, 1991), all species of *Anodonthyla*, except probably for *A. boulengeri*, are known from extremely small ranges only, and in part from only single sites (see maps in Fig. 18 in the Appendix). Because these animals have rather characteristic calls and are not particularly seasonal in their reproduction, we do not believe that these small ranges reflect undersampling but that, as a biological reality, *Anodonthyla* show a very high degree of microendemism. This conclusion is further supported by the genetic substructuring of *A. boulengeri* where the two populations from the offshore islands Nosy Mangabe and Nosy Boraha are differentiated genetically from each other and from

the mainland populations (represented by Foulpointe). Such a microendemic pattern with very small extents of occurrence may be typical for cophylines in general (Wollenberg *et al.*, 2008). This pattern also further reinforces our assumption that the species inventory of *Anodonthyla* is not yet completed, because it predicts additional new species in areas where intensive amphibian inventories followed by an integrative taxonomic approach are so far missing.

The distribution of *Anodonthyla* species diversity, and the phylogeny of the genus, further predicts that forested areas in the Southern Central East and South East of Madagascar most likely yield additional species of this genus. Glaw and Vences (2005) already stated that the center of species diversity and endemism of *Anodonthyla* is in southern Madagascar. This pattern was confirmed by the spatial analysis of Wollenberg *et al.* (2008), whereas several other cophyline lineages, such as *Platypelis/Cophyla* and *Rhombophryne/Stumpffia*, clearly have their centers of diversity and endemism in northern Madagascar. The new species descriptions herein further support this pattern, because four of the newly distinguished species (*A. emilei*, *A. jeanbai*, *A. theoi*, *A. sp. aff. boulengeri* ‘Ranomafana’) as well as the two unconfirmed candidate species from Maharira are from the South East or Southern Central East, while only two newly recognized species (*A. pollicaris* and *A. vallani*) occur in the Northern Central East.

Furthermore, none of the northern distributed species occupy a basal position in the molecular phylogeny: neither the lineage containing the two northernmost distributed species, *A. hutchisoni* and *A. boulengeri*, nor the northern-central distributed species *A. pollicaris* and *A. vallani*. In a more detailed view, *A. pollicaris* is phylogenetically nested in a clade containing three southern species (*A. moramora*, *A. nigrigularis*, and *A. theoi*), and the most parsimonious hypothesis is therefore that its ancestors dispersed northwards into its current northern range. In contrast, *A. hutchisoni*, *A. boulengeri* and *A. vallani* belong to a clade that contains only one southern species (*A. sp. aff. boulengeri* ‘Ranomafana’), and this species is placed in a nested position, which supports that this lineage diversified at least partly in the Northern-Central-East. However, the most basal taxa of *Anodonthyla* (*A. montana*, *A. rouxae*, *A. emilei*, *A. jeanbai*) are southern endemics, all restricted to elevations of 1000 m above sea level or higher, supporting that the initial diversification of *Anodonthyla* took place in the mountains of the South-East or Southern Central East.

Evolution of calls in *Anodonthyla*

As typical for cophylines, the calls of most *Anodonthyla* are long regular series of tonal notes (see Appendix). Although note duration is variable among *Anodonthyla*, in general their notes are shorter than those of other cophylines, such as many representatives of *Cophyla*, *Platypelis*, and *Stumpffia*. This short note duration could be a synapomorphy of *Anodonthyla*. Of the four basal *Anodonthyla*, calls are only known for *A. emilei*, and these have a deviant general structure. To understand call evolution in this genus, obtaining call recordings of *A. jeanbai*, *A. montana* and *A. rouxae* should thus be seen as a priority.

Not considering the deviant *A. emilei*, the calls of *Anodonthyla* vary along mainly three axes: note repetition rate (which depends on inter-note interval duration), note length, and spectral frequency. To the human ear, the most obvious is the temporal difference between calls with fast versus slow note repetition rates. Interestingly, the molecular phylogeny indicates recurrent shifts between low and high note repetition rates in calls, based mainly on three strongly supported sister groups: *A. moramora* with low repetition rate and *A. nigrigularis* with moderately low repetition rate; *A. theoi* with low repetition rate and *A. pollicaris* with high repetition rate; *A. vallani* with low repetition rate and *A. sp. aff. boulengeri* ‘Ranomafana’ with high repetition rate. The factors that influenced these recurrent shifts remain unexplored. Character displacement at first glance appears to be unlikely, because according to current knowledge none of these species pairs occur in sympatry. However, some support for the character displacement hypothesis comes from the fact that the species with the lowest note repetition rate (*A. moramora*, down to 0.6 notes/second) occurs in sympatry with the species with the highest rate (*A. sp. aff. boulengeri* ‘Ranomafana’, up to 3.1 notes/second).

Conservation and IUCN red list assessment

According to the Global Amphibian Assessment for Madagascar and its subsequent updates (Andreone *et al.*, 2005a, 2008b), at present one species of *Anodonthyla* is classified as Endangered (*A. rouxae*), one species as Vulnerable (*A. montana*), one species as Least Concern (*A. boulengeri*) and three species as Data Deficient (*A. hutchisoni*, *A. moramora*, *A. nigrigularis*). Considering the prevalent microendemic pattern of *Anodonthyla* and the fact that our intensive surveys over the past years did not yield a single range

extension of any species but instead led to the discovery of numerous new species, a threatened category in our opinion is warranted for additional species.

No conservation-relevant new data have become available for *Anodonthyla hutchisoni*, *A. montana*, and *A. rouxae*, and we therefore propose no change in the red list status of these species.

Anodonthyla boulengeri, after the revision herein, occupies a much smaller area than previously thought. However, within its extent of occurrence the species is ubiquitous, also in cultivated landscapes, and it occurs in at least one protected area (Nosy Mangabe Special Reserve). We therefore continue considering this species as Least Concern.

Anodonthyla pollicaris is apparently distributed over a relatively small area, but the limits of its distribution are poorly assessed, as are its tolerance of habitat disturbance. We consider a status of Data Deficient for this species as adequate. A similar rationale applies to *A. theoi*; this species was found at a single site only, but nearby localities (*e.g.* Vevembe forest) are only poorly surveyed and the species may be more widespread. In addition, our observations are insufficient to assess whether *A. theoi* is a specialist of more or less intact rainforest or is also able to survive in heavily degraded and secondary forest, or even in cultivated landscape. We therefore propose to consider also this species as Data Deficient.

Anodonthyla nigrigularis has only been found at a limited number of sites (Manantantely, Pic St. Louis, Nahampoana, and low elevations of Andohahela National Park) in very close geographic proximity, whereas the Ambohitantely population assigned to this species has been found to represent a separate species (*A. vallani*). Low-elevation forests in south-eastern Madagascar are under heavy pressure, including those within Andohahela National Park (*e.g.* Ramanamanjato *et al.*, 2002). On the other hand, we have observed *A. nigrigularis* also in secondary forest consisting of mainly eucalypt trees, indicating that this species has a reasonable tolerance to habitat degradation. This pattern is very similar to that of the mantellid frog *Gephyromantis leucocephalus* which also is endemic to South-Eastern lowlands but tolerates to some degree habitat degradation, and which Andreone *et al.* (2005a) included in the Near Threatened category. Based on the same rationale, we propose to also consider *A. nigrigularis* as Near Threatened.

Anodonthyla emilei is morphologically and bioacoustically distinct and yet has not been recorded from localities other than Ranomafana National Park where

it is apparently restricted to higher elevations. This situation is identical to that of the mantellid frog *Gephyromantis runewsweeki*, and following the rationale used for that species by Andreone *et al.* (2008b), we propose a status of Endangered for *A. emilei* because its EOO is less than 5000 km², all individuals are in fewer than five locations, and there is probably a continuing decline in the extent and quality of much of its habitat. We apply the same rationale also to *Anodonthyla moramora*, and propose a status of Endangered to this species as well.

Anodonthyla vallani is restricted to Ambohitantely, an isolated protected area containing a series of forest fragments that are under heavy anthropogenic pressure. Similar to the conclusion drawn (Andreone *et al.*, 2005a) for another microhylid endemic to this site, *Stumpffia helenae*, we propose a status of Critically Endangered for *A. vallani*.

With our proposal, one *Anodonthyla* is now categorized as Critically Endangered, three as Endangered, one as Vulnerable, one as Near Threatened, one as Least Concern, and three as Data Deficient. If the microendemic distribution pattern observed in *Anodonthyla* is confirmed by future studies, also for other cophyline lineages, we predict a similar increase in the number of threatened species also for these. However, it needs to be emphasized that this increase is not due to sharp declines but just to a better taxonomic resolution. Similar to the general situation in Malagasy amphibians (Andreone *et al.*, 2008a), so far no catastrophic declines of *Anodonthyla* have been observed, all species are known from at least one legally protected area, and dense populations of all species have been observed in the wild in the period 2004–2009. The key to their conservation therefore continues to be an effective conservation of the remaining primary habitats, especially within the recently extended network of protected areas (Kremen *et al.*, 2008).

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Appendix

Taxonomic accounts and descriptions of new species

In the following we provide taxonomic notes on nominal species of *Anodonthyla*, and new species descriptions. Note that the diagnoses are organized sequentially, i.e., they do not provide distinctions from those new species described in subsequent sections. A full comparison of most diagnostic characters is given in Table 1.

Anodonthyla pollicaris (Boettger, 1913) bona species (Figs 7a-b)

Holotype. This species was described as *Mantella pollicaris* Boettger, 1913, based on the female holotype specimen SMF 4299 from Anevoka in eastern Madagascar, collected by Sikora in 1902.

Identity. As reported by Glaw and Vences (2005), the type locality of this species could not be located by Blommers-Schlösser and Blanc (1991), but is between Toamasina (Tamatave) and Tanaramé (Boettger, 1913: 273) and may correspond to a village (18°56'S, 48°28'E, 936 m a.s.l.) with this name close to Andasibe. Although the holotype is a female, some of its morphological characters agree with specimens collected at Andasibe, such as the relatively large tympanum (Table 2), which however is not clearly visible and appears to be smaller in at least two other comparative specimens. Our phylogenetic data (Figs 1-2) provide clear evidence that the Andasibe specimens are to be considered as distinct species, different from all currently recognized *Anodonthyla*: Although they roughly agree in general morphology and note repetition rate with *A. boulengeri*, they are placed sister to a population from Manombo which has a much slower note repetition rate and several morphological differences (described as *A. theoi* below), and these two species further belong to a more inclusive clade with *A. moramora* and *A. nigrigularis*, also characterized by slow to very slow note repetition rates. There are no clear morphological characters that would allow to exclude conspecificity of the type of *pollicaris*

Table 1. Summary of the most important diagnostic characters differentiating all *Anodonthyla* species as recognized herein. Species are ordered approximatively according to morphological similarity.

	A. <i>boulengeri</i>	A. <i>pollicaris</i>	A. <i>sp.aff. boulengeri</i>	A. <i>hutchisoni</i>	A. <i>jeanbai</i>	A. <i>moramora</i>	A. <i>nigrigularis theoi</i>	A. <i>vallani</i>	A. <i>emilei</i>	A. <i>rouxae</i>	A. <i>montana</i>
Male SVL [mm]	15-22	16-19	17-19	20-23	14-20	15-17	20-22	18-20	23-24	24-34	32-34
Humeral spine	no	grey	grey	grey	no	no	grey	grey	no	yes	no
Ventral colour	grey	no	no	no	with yellow	often greenish	grey	grey	grey	grey	grey
Copper colour in iris	no	no	no	no	yes	yes	no	no	yes	no	no
Blackish vocal sac	sometimes	no	no	no	no	no	yes	yes	no	no	no
Tympanum	often indistinct	sometimes indistinct	moderately distinct	moderately distinct	distinct	moderately distinct	moderately indistinct	sometimes indistinct	often indistinct	moderately distinct	distinct
Anterior dorsolateral ridge	absent	absent	sometimes weakly recognizable	absent	present	absent	absent	absent	absent	absent	absent
calls as short series (<5 s)	no	no	no	no	unknown	no	no	no	yes	unknown	unknown
note repetition rate [1/s]	1.8-2.5	2.6-2.9	2.6-3.1	1.0-1.3	unknown	0.6-0.9	1.0-1.6	0.8-0.9	5.1-5.5	unknown	unknown
note duration [ms]	18-46	49-86	49-91	10-45	unknown	47-80	60-117	153-230	58-81	unknown	unknown
dominant frequency [Hz]	3500-4300	4000-4500	4080-4350	3100-3200	unknown	5400-5700	3600-4500	6040-6100	2500-2660	unknown	unknown

Table 2. Morphometric measurements (all in mm) of types and comparative specimens of species of *Anodonthyla* (except *A. hutchisoni*). For abbreviations of measured variables, see Materials and methods; further abbreviations used: M (male); F (female); HT (holotype); PT (paratype); LT (lectotype). Tympanum diameter (TD) values in parentheses indicate that the tympanum was not distinct. RHL (relative hindlimb length) is coded as follows: Tibiotarsal articulation reaches 1, forelimb insertion; 2, between forelimb insertion and tympanum; 3, tympanum; 4, between tympanum and eye; 5, posterior eye corner; 6, eye center; 7, anterior eye corner. Some details of localities are abbreviated as well: NP, National Park; SR, Special Reserve; FS, forestry station; IE, between Isaka and Eminiminy; M, Mahairra; S, Samalotra; V, Vohiparara. The holotype of *A. boulengeri* was described from 'Madagascar' without precise locality data.

ZSM Number	Locality	Sex	Status	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FL	TIBL	PREP	RHL
<i>A. boulengeri</i>																			
NMBA 1448	unknown	F	HT	20.3	6.6	6.4	1.0	2.1	1.4	1.4	1.8	12.7	5.5	27.3	12.1	7.7	9.9	---	3
ZSM 407/2005	Nosy Mangabe	M		20.3	6.6	6.7	1.5	2.5	1.6	1.0	2.2	13.5	5.9	28.8	13.4	8.4	9.4	2.0	5
ZSM 406/2005	Nosy Mangabe	F		22.6	7.8	7.1	1.7	2.8	1.6	1.2	2.1	14.3	6.0	30.9	13.3	8.4	9.8	no	3
ZFMK 52775	Nosy Mangabe	M		22.0	7.5	6.4	(1.3)	2.7	1.5	1.1	2.0	14.6	6.8	32.1	14.5	9.1	10.0	1.8	3
ZFMK 52781	Nosy Mangabe	M		21.9	7.0	6.3	(1.5)	2.4	1.6	1.2	2.3	14.0	6.8	30.5	14.1	9.0	9.8	1.6	3
ZFMK 52783	Nosy Mangabe	M		18.0	5.7	5.7	---	2.0	1.3	0.9	1.6	12.0	5.6	27.1	12.1	7.7	8.6	1.6	5
ZFMK 52782	Nosy Mangabe	M		22.3	7.0	6.5	(1.5)	2.1	1.5	1.0	2.2	12.0	6.4	31.0	14.2	9.1	9.7	1.7	3
ZSM 216/2006	Nosy Boraha	M		18.2	5.6	5.6	1.3	2.1	1.0	1.0	1.8	10.5	4.6	23.1	10.0	6.3	7.8	1.3	2
ZSM 218/2006	Nosy Boraha	M		16.7	5.1	5.5	1.2	1.9	1.4	1.0	1.9	10.0	5.1	23.4	10.4	6.4	7.6	1.4	3
ZSM 217/2006	Nosy Boraha	M		15.3	5.3	5.3	(1.0)	2.0	1.3	1.2	1.9	10.3	4.5	22.0	9.9	6.0	7.3	1.4	5
ZSM 219/2006	Nosy Boraha	M		17.1	5.2	5.5	(1.0)	1.9	1.2	1.2	1.6	11.1	5.1	24.2	10.6	6.6	7.7	1.5	3
ZSM 215/2006	Nosy Boraha	M		17.5	5.6	5.7	(1.0)	2.0	1.4	0.9	1.8	10.5	4.9	23.0	10.7	6.9	7.5	miss.	2
ZFMK 52784	Nosy Boraha	M		15.7	5.1	5.2	1.0	1.6	1.3	1.0	1.7	9.4	4.1	21.0	9.6	6.4	6.9	1.2	3
ZFMK 52786	Nosy Boraha	M		17.3	5.5	5.5	0.9	1.9	1.3	1.0	1.9	11.2	5.3	24.2	11.1	6.8	7.5	1.4	3
ZFMK 52785	Nosy Boraha	F		19.2	5.7	5.7	1.1	2.2	1.3	0.9	1.8	10.6	4.4	24.9	10.4	6.3	7.7	---	3
ZSM 264/2002	Foulpointe	M		18.0	5.4	5.2	1.1	2.1	1.2	1.0	1.9	11.6	4.9	24.6	11.3	7.3	7.8	1.6	3
<i>A. sp. aff. boulengeri</i>																			
ZSM 2277/2007	Ambohitsara	M		18.6	5.7	5.7	1.7	2.0	1.4	1.4	1.9	11.8	5.5	27.8	13.0	8.1	9.0	1.7	6
ZFMK 62313	Ranomafana	M		18.7	5.6	5.4	1.0	2.0	1.3	0.9	1.7	11.2	5.2	28.3	12.8	8.0	8.8	1.6	5
ZMA 19430	Ranomafana	M		17.3	5.0	4.6	0.9	2.0	1.2	1.0	1.8	11.3	5.0	26.9	12.0	7.6	8.2	1.7	5
ZSM 642/2003	Ranomafana village	M		17.4	5.0	5.3	1.1	2.0	1.3	0.8	1.8	11.4	5.0	26.7	11.7	7.2	9.2	1.5	7
ZSM 643/2003	Ranomafana village	F		18.2	5.1	5.4	1.3	1.9	1.2	1.1	1.5	13.2	5.4	29.6	13.2	8.2	8.9	---	6
<i>A. pollicaris</i>																			
SMF 4299	Anevoka	F	HT	21.2	6.2	6.1	1.5	2.3	1.3	1.0	2.2	12.6	5.3	29.2	13.0	8.4	9.5	---	3
ZFMK 53742	Andasibe	M		19.0	5.9	5.6	1.3	1.7	1.3	1.0	1.7	10.5	5.4	25.6	11.5	7.1	8.3	1.4	3
ZFMK 52780	Andasibe	F		19.4	5.7	5.8	1.4	1.9	1.5	1.1	1.6	11.6	5.4	27.7	12.6	8.0	8.5	---	3
ZFMK 62215	Andasibe	M		17.8	5.8	5.5	1.2	2.0	1.6	1.0	1.8	10.6	5.1	27.5	12.6	8.0	8.5	1.7	6
ZFMK 62222	Andasibe	M		16.2	5.3	5.4	1.0	1.6	1.0	0.7	1.6	11.1	4.7	25.3	11.5	7.3	8.3	1.6	5
ZSM 408/2005	Andasibe FS	M		18.6	5.7	5.6	(1.1)	2.1	1.0	0.9	1.8	11.4	5.6	26.5	11.3	7.9	7.9	1.8	3
ZSM 409/2005	Andasibe FS	M		16.5	4.9	5.1	(1.2)	1.8	1.2	1.1	1.7	9.4	5.0	24.9	11.0	7.0	7.6	1.7	3
<i>A. theoi</i>																			
ZSM 2273/2007	Manombo SR	M	PT	18.7	5.6	5.6	1.1	2.1	1.3	1.0	1.9	11.3	5.5	25.5	11.4	7.0	7.9	1.9	2
ZFMK 89186	Manombo SR	M	PT	18.3	5.3	5.3	1.1	2.0	1.2	1.0	1.9	11.6	5.5	25.9	11.5	7.5	8.1	1.8	3
ZSM 2275/2007	Manombo SR	M	HT	18.9	5.5	5.3	(1.2)	2.5	1.1	1.1	1.9	11.8	5.9	27.2	12.0	7.4	8.1	1.8	2
ZSM 2276/2007	Manombo SR	M	PT	19.5	5.5	5.5	(1.5)	2.5	1.2	0.9	1.7	11.9	5.3	25.0	11.4	7.7	8.3	1.8	2
<i>A. vallani</i>																			
ZSM 86/2005	Ambohitantely SR	M	HT	22.8	8.0	7.0	1.3	2.7	1.3	1.3	2.3	13.9	7.2	33.8	15.6	10.5	10.8	2.3	3

ZSM 87/2005	Ambohitantely SR	M	PT	24.1	8.1	7.4	1.3	2.5	1.6	1.5	2.4	14.8	7.0	35.0	15.8	10.4	10.5	2.5	3
<i>A. jecoubai</i>																			
ZSM 88/2005	Andohahela NP	M	HT	19.9	5.7	6.0	1.4	2.1	1.0	1.0	1.8	11.0	5.6	26.6	13.0	8.4	8.3	2.2	3
ZSM 89/2005	Andohahela NP	M	PT	18.6	5.5	5.7	1.3	2.0	1.1	1.0	1.8	11.0	5.1	26.2	12.7	8.2	7.9	2.0	3
ZSM 90/2005	Andohahela NP	F	PT	19.1	5.7	5.8	1.6	2.0	1.4	1.3	2.0	11.0	4.8	25.4	12.0	7.7	7.8	no	1
ZSM 91/2005	Andohahela NP	F	PT	19.3	6.1	6.2	1.4	2.0	1.3	1.2	1.8	10.7	4.7	25.5	12.1	7.8	8.0	no	2
ZSM 92/2005	Andohahela NP	M	PT	16.2	5.1	5.4	1.2	2.0	1.2	1.0	1.7	9.3	4.4	23.7	10.9	7.0	7.4	1.8	3
ZSM 93/2005	Andohahela NP	M	PT	14.9	4.7	4.9	1.3	1.7	0.9	0.9	1.6	8.9	3.9	23.8	10.3	6.4	7.3	1.6	5
ZSM 94/2005	Andohahela NP	M	PT	14.2	4.4	5.1	1.4	1.8	1.0	0.8	1.7	7.9	3.3	18.9	9.1	5.7	6.5	1.4	3
ZSM 95/2005	Andohahela NP	F	PT	18.3	5.4	5.7	1.4	1.9	1.2	1.0	1.8	10.6	4.8	24.7	11.4	7.1	7.7	no	3
ZSM 96/2005	Andohahela NP	M	PT	18.7	5.3	5.6	1.3	1.9	1.5	1.3	2.0	11.1	5.7	26.4	12.4	8.0	7.9	2.2	2
ZFMK 89187	Andohahela NP	M	PT	18.9	5.6	6.2	1.2	1.9	1.0	1.1	1.7	11.0	5.6	26.9	12.2	8.0	8.1	2.2	3
<i>A. nigrigularis</i>																			
ZFMK 53745	Nahampoana	M	HT	20.7	6.8	6.0	1.1	1.9	1.3	0.9	2.2	13.0	6.2	31.4	14.0	9.0	9.8	1.8	3
ZSM 553/1999	Nahampoana	M	PT	21.1	6.5	6.6	1.5	2.3	1.6	1.0	2.0	11.9	6.0	31.1	13.9	8.9	9.1	1.8	3
ZSM 87/2004	Andohahela NP (IE)	M		21.4	6.7	6.9	1.5	2.7	1.4	1.2	2.5	13.2	6.5	32.6	14.9	9.4	10.0	2.4	5
ZSM 88/2004	Andohahela NP (IE)	M		20.7	6.9	6.9	1.5	2.6	1.5	1.5	2.5	14.0	6.4	31.9	14.2	9.0	10.0	2.0	5
ZSM 92/2004	Andohahela NP (IE)	M		20.8	6.7	7.4	1.8	2.6	1.3	1.1	2.2	12.5	6.4	30.1	14.3	9.1	9.5	2.1	3
ZSM 94/2004	Andohahela NP (IE)	M		21.7	6.9	7.1	1.2	2.6	1.6	1.0	2.2	14.1	6.9	30.8	15.1	9.4	9.7	1.8	3
ZSM 390/2005	Manantantely	M		19.2	6.0	6.5	1.3	2.3	1.6	1.4	1.9	12.1	5.5	28.5	12.8	8.0	8.6	1.8	3
ZSM 391/2005	Manantantely	M		19.9	6.7	6.1	1.5	2.2	1.4	1.3	2.2	12.5	5.5	27.7	12.6	7.9	8.7	1.5	4
ZSM 164/2004	Manantantely	F		21.7	6.9	6.4	1.5	2.3	1.4	1.3	1.8	14.4	5.6	31.8	14.0	8.7	9.7	no	3
<i>A. moramora</i>																			
ZFMK 62308	Ranomafana NP	M	PT	16.0	5.2	5.2	1.0	1.8	1.1	0.9	1.7	10.7	5.0	24.1	11.0	6.8	7.6	1.6	5
ZFMK 62275	Ranomafana NP (V)	M	PT	15.9	5.0	5.0	1.2	1.5	1.3	1.0	1.5	20.0	4.3	22.5	10.2	6.7	7.0	1.6	6
ZFMK 62276	Ranomafana NP (V)	M	PT	15.1	5.0	5.0	1.2	1.5	1.2	1.0	1.6	10.2	4.5	22.2	10.0	6.6	7.3	1.5	5
ZFMK 62309	Ranomafana NP	F	PT	15.4	5.0	4.8	0.9	1.7	1.0	1.0	1.7	10.4	4.3	22.8	10.5	6.6	7.2	---	6
ZMA 19428	Ranomafana NP (V)	M	PT	15.8	5.0	5.2	1.1	1.6	1.0	1.0	1.9	10.1	4.9	23.0	10.2	6.4	7.2	1.9	3
ZMA 19429	Ranomafana NP (V)	M	PT	16.0	5.0	5.2	1.0	1.6	0.9	1.0	1.9	9.5	4.9	22.3	11.0	6.7	7.2	1.6	4
ZSM 705/2003	Ranomafana NP (V)	M	PT	15.0	5.0	5.0	1.1	2.0	1.1	0.9	1.8	9.7	4.5	22.2	10.0	6.1	7.2	1.9	6
ZSM 706/2003	Ranomafana NP (V)	M	PT	16.5	5.5	5.4	1.1	2.0	1.1	1.0	2.0	10.4	5.0	24.4	10.7	6.6	7.5	1.7	5
ZSM 744/2003	Ranomafana NP (V)	M	HT	15.9	5.0	5.0	1.1	2.0	1.2	1.1	1.8	10.4	5.0	23.2	10.6	6.8	7.3	1.8	6
<i>A. rouxae</i>																			
MNHN 1973.666	Chaînes Anosyennes	M	HT	28.3	9.2	8.6	1.3	3.0	2.0	1.6	3.0	17.8	9.2	40.2	20.0	13.1	11.5	2.0	2
ZSM 98/2005	Andohahela NP	M		33.9	11.2	10.6	2.1	3.7	2.2	1.5	2.8	21.5	10.8	46.0	23.9	16.3	13.6	2.5	3
<i>A. montana</i>																			
MNHN 1924.107	Andringitra	F	LT	33.0	11.2	10.0	2.5	3.8	2.2	2.2	3.4	19.4	8.9	41.6	20.3	13.3	13.4	---	1
<i>A. emilei</i>																			
ZSM 673/2003	Ranomafana NP (S)	M	HT	24.2	8.6	8.1	1.7	2.9	1.7	1.7	2.4	15.4	7.5	34.5	16.1	10.5	10.6	2.3	3
ZSM 674/2003	Ranomafana NP (S)	M	PT	23.8	8.5	7.9	(1.6)	2.8	1.6	1.5	2.6	15.2	7.6	33.3	15.6	9.6	10.1	2.0	2
ZFMK 89185	Ranomafana NP (M)	M	PT	25.7	8.5	8.1	(1.6)	3.2	1.5	1.5	2.5	17.4	8.4	37.2	16.9	11.3	11.2	1.8	3
ZSM 366/2004	Ranomafana NP (M)	M	PT	22.7	8.2	7.8	(1.5)	3.2	1.4	1.5	2.4	14.9	7.0	33.1	15.2	9.9	9.9	1.4	3
ZSM 367/2004	Ranomafana NP (M)	M	PT	25.3	9.0	8.3	1.6	3.0	1.6	1.7	2.4	17.3	8.7	37.4	17.4	11.8	11.2	2.1	3
ZSM 368/2004	Ranomafana NP (M)	M	PT	26.5	9.2	8.4	(1.9)	2.9	1.7	1.6	2.8	17.0	8.1	36.4	17.3	11.4	10.8	1.9	2
ZSM 369/2004	Ranomafana NP (M)	M	PT	29.1	9.6	8.8	(1.9)	3.4	1.8	1.7	2.6	18.3	9.2	39.9	18.8	12.5	12.1	2.2	2



Fig. 7a-f. Specimens in life, in dorsolateral and ventral view, of *Anodonthyla pollicaris* from Andasibe (A-B); *A. boulengeri* from Nosy Mangabe (C-D); and Nosy Boraha (E-F) (all males).

with this distinct species from the Andasibe region, and as a measure of taxonomic parsimony we therefore resurrect the name *Anodonthyla pollicaris* for this species.

Diagnosis. A moderately small arboreal frog with a fast repetition rate of advertisement calls, assigned to *Anodonthyla* on the basis of the presence of a distinct prepollex in males. Distinguished from all other

Anodonthyla by a significant genetic differentiation. Further distinguished from *A. montana* and *A. rouxae* by a clearly smaller body size, and from *A. moramora* by a larger body size (Tables 1 and 2). Further distinguished from *A. moramora*, *A. hutchisoni*, and *A. nigrigularis* by a distinctly faster repetition rate of advertisement calls. The species is most similar to *A. bouleengeri*, and reliable morphological characters to distinguish these two species are unknown. However, the two species can be distinguished by subtle differences in advertisement calls, namely a faster note repetition rate and longer note duration in *A. pollicaris* (see Table 3 and below).

Redescription. Based on ZSM 408/2005 (ZCMV 2207), an adult male from Andasibe. Specimen in good state of preservation (left arm removed as tissue sample for molecular analysis). SVL 19.9 mm (for other measurements see Table 2). Body moderately slender; head very slightly wider than long, not wider than body; snout slightly pointed in dorsal view, rounded in lateral views; nostrils directed laterally, slightly protuberant, of almost same distance to tip of snout and to eye; canthus rostralis indistinct, concave; loreal region straight; tympanum moderately distinct, rounded, its diameter 52% of eye diameter; supratympanic fold recognizable; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; maxillary teeth very poorly recognizable; vomerine teeth absent; choanae rounded. Arms moderately thickened; subarticular tubercles well recognizable at the base of fingers; outer metacarpal tubercle distinct; prepollex distinct, extending from the area generally occupied by the inner metacarpal tubercle to a point at the base of digital pad of first finger; tips of first finger and prepollex not diverging; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, inner finger rudimentary with rounded disk, disks of fingers 2-4 distinctly enlarged, of triangular shape; keratinized nuptial pads absent, but a distinctly thickened less pigmented area on inner side of arm. Hindlimbs slender; tibiotarsal articulation reaching tympanum when hindlimb adpressed along body; TL 42% of SVL; lateral metatarsalia strongly connected; metatarsal tubercles poorly recognizable; no webbing between toes; relative length of toes $1 < 2 < 5 < 3 < 4$; third toe distinctly longer than fifth. Skin on dorsum and ventral surface smooth.

Table 3. Basic bioacoustic parameters among specimens of *Anodonthyla* species. Temporal measurements are given in milliseconds (ms) as range, with mean \pm standard deviation in parentheses.

Species	Locality	Recording date	Temperature	Note duration [ms]	Inter-note interval duration [ms]	Dominant frequency [Hz]	Note repetition rate [notes/s]
<i>A. emilei</i>	Ranomafana (Samalaoatra)	18.I.2003	20.6°C	58-81 (65 \pm 7, N = 26)	103-134 (117 \pm 11, N = 28)	2500-2660	5.1-5.5
<i>A. vallani</i>	Ambohitantely	17.I.2005	---	154-236 (188 \pm 26, N = 15)	705-1016 (824 \pm 98, N = 14)	2850-2900	0.8-1.0
<i>A. theoi</i>	Manombo	23.II.2007	---	153-230 (184 \pm 28, N = 16)	880-1297 (1030 \pm 115, N = 11)	6040-6100	0.8-0.9
<i>A. moramora</i>	Ranomafana	29.II.1996	22°C	47-80 (66 \pm 11, N = 27)	1468-2375 (1597 \pm 183, N = 24)	5400-5700	0.6-0.9
<i>A. pollicaris</i>	Andasibe	30.I.1996	22.5°C	49-55 (52 \pm 2, N = 11)	268-389 (305 \pm 35, N = 10)	4200-4500	2.6-2.9
<i>A. pollicaris</i>	Ankeniheny	18.II.1994	22°C	61-86 (72 \pm 8, N = 13)	283-352 (313 \pm 17, N = 12)	4000-4200	2.7
<i>A. sp. aff. bouleengeri</i>	Kianjavato	24.I.2003	---	77-91 (83 \pm 5, N = 14)	240-302 (270 \pm 17, N = 12)	4080-4120	2.6-3.1
<i>A. sp. aff. bouleengeri</i>	Ranomafana	29.II.1996	22°C	49-80 (65 \pm 11, N = 16)	268-299 (283 \pm 9, N = 14)	4100-4350	2.8-3.1
<i>A. bouleengeri</i>	Nosy Mangabe	12.III.1991	ca. 25°C	20-46 (35 \pm 7, N = 17)	282-472 (370 \pm 50, N = 15)	3500-3750	2.5
<i>A. bouleengeri</i>	Nosy Mangabe	12.III.1991	ca. 25°C	18-29 (22 \pm 3, N = 12)	413-677 (482 \pm 80, N = 11)	3500-3700	2.0
<i>A. bouleengeri</i>	Nosy Boraha	4-7.III.1991	ca. 25°C	24-28 (26 \pm 2, N = 7)	562-654 (611 \pm 39, N = 6)	4100-4300	1.8
<i>A. bouleengeri</i>	Nosy Boraha	4-7.III.1991	ca. 25°C	35-37 (37 \pm 1, N = 7)	867-1064 (971 \pm 78, N = 5)	---	---
<i>A. nigrigularis</i>	Nahampoana	4.I.1991	---	60-117 (95 \pm 20, N = 10)	642-797 (694 \pm 51, N = 8)	4500	1.3-1.4
<i>A. nigrigularis</i>	Manantantely	23.I.2005	29°C	71-85 (78 \pm 4, N = 10)	505-679 (565 \pm 62, N = 10)	4400-4500	1.5-1.6
<i>A. nigrigularis</i>	Andohahela	1992	---	65-78 (69 \pm 4, N = 14)	753-1014 (855 \pm 87, N = 11)	3600-3800	1.0-1.1

(rec. D. Vallan)

Colour. After four years in preservative, dorsum and head dark brown marbled with several distinct beige markings: a thin bar between the eyes, a W-shaped marking on the neck, a broad, irregular and slightly triangular crossband at middorsum, and an oval spot on posterior dorsum. Flanks marbled brown and beige. Tympanic region light, bordered by a dark supratympanic region. Forelimbs without distinct dark crossband, hindlimbs with distinct dark crossbands, bordered by beige. Cloacal region blackish. Throat brown, chest, belly and ventral parts of limbs dirty yellowish to grey with scattered brown pigment. Thickened ventral sides of arms less intensely pigmented.

Advertisement call. Based on data in Glaw and Vences (2005) and provided here as comparative oscillograms (Fig. 3) and in Table 3, the calls of *A. pollicaris* are characterized by a relatively fast note repetition rate of 2.6–2.9 notes per second and a note length of 49–86 ms. Note repetition rate is thus slightly higher than in *A. boulengeri* (1.8–2.5 notes/second) although the recordings of *A. pollicaris* calls were obtained at lower temperatures (Table 3).

Natural history. Calling males of *A. pollicaris* were found at night in mid-altitude rainforest, 1–3 m high on tree trunks and in a water-filled hole in a tree fern (Glaw and Vences, 1994; further own observations).

Distribution. Based on genetic and bioacoustic data, this species is known from (1) the type locality Anevoka, (2) Andasibe, including Analamazoatra/Mantadia National Park, and (3) Ambavaniasy. Based on bioacoustic data only (Fig. 3), the species is also known from Ankeniheny.

Anodonthyla boulengeri Müller, 1892 (Figs 7c–f)

Holotype. This species was described based on a female holotype (NMBA 1448) originating from Madagascar, without further locality information.

Identity. Historically, especially populations from lowlands in the Malagasy east coast were assigned to this species (Blommers-Schlösser, 1975; Blommers-Schlösser and Blanc, 1991) although also records from Andasibe, Ranomafana and Andohahela were published which according to our data refer to populations that are not conspecific with the Northern Central East coast populations. As the taxonomically most parsimonious solution, we here propose to continue considering populations from the Northern Central East coast (here represented by Nosy Mangabe, Foulpointe, and Nosy Boraha) as *A. boulengeri*. This is also in general

agreement with morphological data. Although the holotype of *A. boulengeri* is a female and most other specimens studied by us are males, in general *Anodonthyla* appear to show only a limited sexual size dimorphism, if any. The SVL of the *A. boulengeri* holotype (20.3 mm), its rather well visible but small tympanum, and other morphometric characters are in agreement with, for example, the studied male specimen from Foulpointe (ZSM 264/2002). For diagnostic characters of *A. boulengeri*, see Table 1.

Genetic differentiation. The three populations studied herein show a considerable genetic divergence which amounts to 1.1% uncorrected 16S divergence between Foulpointe and Nosy Mangabe and 1.6% between Nosy Boraha (sequenced specimen: ZSM 219/2006; not included in tree because a different non-overlapping fragment of the 16S rRNA gene is available for this individual) and the two other populations. Two individuals sequenced from Nosy Mangabe (ZSM 407/2005 and UADBA-ZCMV 2141) had identical sequences.

Advertisement call. Based on data given in Glaw and Vences (2005) and shown here in Table 3 and Fig. 3, the two populations of *A. boulengeri* studied for their advertisement calls (Nosy Boraha and Nosy Mangabe) have very similar call parameters. They are characterized by high note repetition rates of 1.8–2.5 per second, and very short note duration of 18–46 ms. Calls of *A. hutchisoni*, which occurs geographically close to the Nosy Mangabe population, differ by a lower note repetition rate of 1.0–1.3 notes per second. In contrast, populations from the Andasibe and Ranomafana regions, which we here consider as two species distinct from *A. boulengeri*, differ by longer notes of 49–86 ms duration.

Natural history. Calling males of *A. boulengeri* are found at night at perch heights of 1–3 m on tree trunks in rainforest (Nosy Mangabe) but also commonly in degraded forest, and in secondary vegetation with trees, in cultivated landscapes (Foulpointe and Nosy Boraha). Reproduction takes place in tree holes, and in leaf axils of *Ravenala* and *Typhonodorum* (observations from Foulpointe, Nosy Mangabe: Blommers-Schlösser 1975; Glaw and Vences 1994).

Distribution. Based on molecular and bioacoustic data available, three populations can be assigned to *A. boulengeri*: Foulpointe, Nosy Mangabe, and Nosy Boraha. It can be assumed that other populations reported by Blommers-Schlösser and Blanc (1991) from the same coastal area belong to this species as well: Tampolo, Fenoarivo, Ivoloina, and Vokaraharo.

Anodonthyla sp. aff. *boulengeri* ‘Ranomafana’ (Fig. 8)

Identity. As reported by Glaw and Vences (2005), in Ranomafana, forests at higher elevations (roughly above 900 m) are occupied mainly by *Anodonthyla moramora*, whereas at lower elevations, populations of a different *Anodonthyla* occur that are morphologically and bioacoustically similar to *A. boulengeri* (and *A. pollicaris*). The molecular tree shows, however, that this form from Ranomafana is genetically highly distinct from *A. boulengeri* and *A. pollicaris*, and is sister to a morphologically and bioacoustically divergent population from Ambohitantely (described below as *A. vallani*). In addition, the calls from the Ranomafana region show some subtle differences to *A. boulengeri*. It therefore seems to be clear that the populations from the Ranomafana region previously assigned to *A. boulengeri* in fact belong to a distinct, undescribed species. We here refrain from describing this new species because the data available to us are too fragmentary: call recordings and DNA sequences partly do not refer to the same individuals and sites, and many of the recorded and sequenced individuals were not available for morphological study. In general, a future detailed revision of the *Anodonthyla* populations characterized by fast note repetition rates is necessary, using a combined genetic and bioacoustic assessment of populations from a more comprehensive geographic coverage, and including contact zones between genetically divergent forms still included in *A. boulengeri* (e.g. Nosy Boraha vs. Nosy Mangabe and Foulpointe; see above). We thus here provide only preliminary data on the populations from the Ranomafana region which we consider as confirmed candidate species following the terminology of Vieites *et al.* (2009).

Diagnosis. A moderately small arboreal frog with a fast repetition rate of advertisement calls, assigned to *Anodonthyla* on the basis of the presence of a distinct prepollax in males. Distinguished from all other *Anodonthyla* by a significant genetic differentiation. Further distinguished from *A. montana* and *A. rouxae* by a clearly smaller body size, and from the sympatric *A. moramora* by a larger body size (Table 2). Further distinguished from *A. moramora*, *A. hutchisoni*, and *A. nigrigularis* by a distinctly faster repetition rate of advertisement calls. The species is most similar to *A. boulengeri* and *A. pollicaris* and reliable morphological characters to distinguish it from these two species are unknown. However, *A. sp. aff. boulengeri* ‘Ranomafana’ can be distinguished from *A. boulengeri* by a faster note repetition rate and longer note dura-

tion, while its advertisement calls are very similar to those of *A. pollicaris* (see Table 1 and 3, and call descriptions in the sections below).

Advertisement call. Call recordings are available from Ranomafana (Glaw and Vences, 2005) and from near Kianjavato (this paper, Figs 3 and 9), and the calls from the two localities are concordant in their temporal and spectral characters (Table 3). They have a high note repetition rate of 2.6-3.1 notes per second and a note duration of 49-91 ms. Note repetition rate is thus higher than in *A. boulengeri* (1.8-2.5 notes/second) although the recordings of calls of *A. sp. aff. boulengeri* ‘Ranomafana’ were obtained at lower temperatures (Table 3).

Natural history. Calling males of this species were observed at night in rainforest, but also in cultivated landscape far from forest (gardens of Ranomafana village), on tree trunks at perch heights of 1.5-3 m.

Distribution. The species is probably widespread in low elevations in the Southern Central East of Madagascar. Bioacoustically identified specimens are from (1) Ranomafana National Park including Ambatolahy and Talatakely and (2) near Kianjavato, genetic data are available from a specimen from (3) Ranomafana village (UADBA-ZCMV 13), from field observations, a DNA sequence and a photograph from (4) Mahakajy private reserve, and (5) from genetically divergent specimens from Ambohitsara (Fig. 8C).

Anodonthyla emilei sp. nov. (Fig. 10)

Holotype. ZSM 673/2003 (field number FG/MV 2002-0267), adult male, collected at Samalaoatra (21°14.113’S, 47°23.767’E, ca. 1000 m a.s.l.), Ranomafana National Park, Fianarantsoa Province, Southern Central East of Madagascar, on 18 January 2003 by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas and D. R. Vieites.

Paratypes. ZSM 674/2003 (field number FG/MV 2002-0268), adult male, same data as holotype; ZSM 366-369/2004 (field numbers ZCMV 214-216, 300) and ZFMK 89185 (=ZSM 365/2004, field number ZCMV 213), five adult males, collected at Ranomafana National Park (Maharira, base camp), 21°19.547’S, 47°24.147’E, about 900-1000 m a.s.l., Fianarantsoa Province, Southern Central East of Madagascar, on 24 January 2004 by M. Vences, I. De la Riva, E. Rajeriarison and T. Rajofiarison.

Justification. This species occupies a largely isolated position in the phylogenetic tree, with very high genetic divergences to all other *Anodonthyla* (16S pairwise distances 8.3-13.4%), and furthermore has

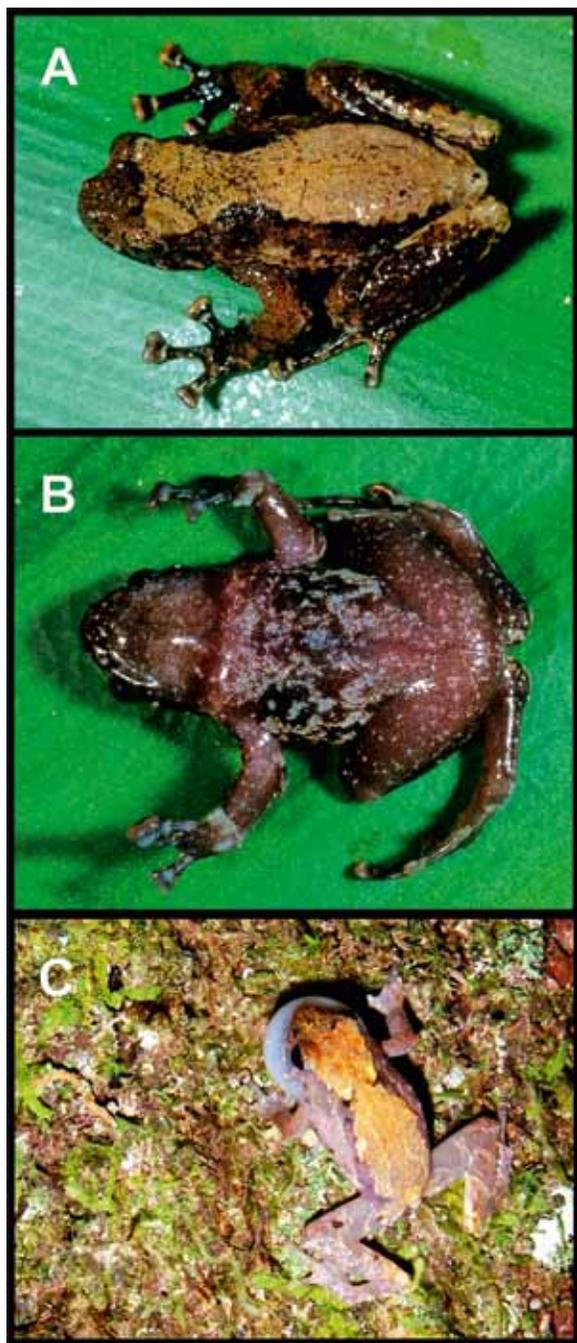


Fig. 8a-c. Male specimen of *Anodonthyla* sp. aff. *boulengeri* 'Ranomafana' in life (ZSM 642/2003) from Ranomafana in dorsolateral and ventral view (A-B); and a further specimen from Mahakajy private reserve (near Ranomafana) photographed at night calling (C; not collected). Although both specimens show a large light patch on the dorsum, this colour pattern is not typical for all individuals of this species.

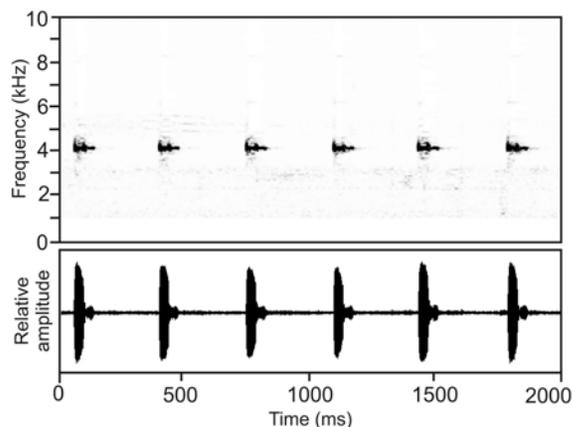


Fig. 9. Spectrogram and waveform of a part of a call series of *Anodonthyla* sp. aff. *boulengeri* 'Ranomafana', recorded near Kianjavato on 24 January 2003.

the most divergent call of all *Anodonthyla*. Its species status is therefore beyond question.

Diagnosis. A medium-sized species of *Anodonthyla* assigned to the genus on the basis of the presence of a distinct prepollex in males. Distinguished from all other *Anodonthyla* by a significant genetic differentiation, and from all species (except *A. montana* and *A. rouxae* where the calls are unknown) by advertisement calls which are a short series of fastly repeated short notes (vs. slower repetition of calls, with series that can last for at least several minutes). *A. emilei* is further distinguished from *A. montana* by smaller size (male SVL 24-27 vs. 32-34 mm), a less strongly developed supratympanic fold, and less distinct tympanum; from *A. rouxae* by the absence of distinct humeral spines in males (vs. presence) and generally by the presence of some coarse tubercles on body (vs. smooth skin); and from *A. rouxae* and *A. montana* by the presence of at least a slight shade of copper in the iris colouration (vs. absence). *A. emilei* is distinguished from *A. boulengeri*, *A. sp. aff. boulengeri* 'Ranomafana', *A. hutchisoni*, *A. moramora*, *A. nigrigularis*, and *A. pollicaris* by a larger body size (male SVL 24-27 vs. 15-23 mm). Many specimens of *A. emilei* show a strongly contrasted colouration and the presence of orange dorsal patches of different size, not known thus far from other species in this genus. In males of *A. emilei*, the forelimbs are furthermore less distinctly enlarged than in various other species of *Anodonthyla*, and the tympanum is usually less distinct.

Description of holotype. Specimen in excellent state of preservation (fourth finger of right hand removed as tissue sample for molecular analysis). SVL

24.2 mm (for other measurements see Table 2). Body moderately slender; head wider than long, not wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protuberant, in same distance to tip of snout and to eye; canthus rostralis moderately distinct, concave; loreal region straight; tympanum indistinct, rounded, its diameter 59% of eye diameter; supratympanic fold indistinct; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; small maxillary teeth present; vomerine teeth absent; choanae rounded. Arms slender, only slightly thickened; subarticular tubercles only recognizable at the base of fingers; outer metacarpal tubercle indistinct; prepollex medium-sized and distinct, extending from the area generally occupied by the inner metacarpal tubercle to a point below digital pad of first finger; tips of first finger and prepollex almost parallel; fingers without webbing; relative length of fingers $1 < 2 = 4 < 3$, inner finger rudimentary, with rounded, slightly enlarged disk, disks of fingers 2-4 distinctly enlarged, of triangular shape; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching the tympanum when hindlimb adpressed along body; TL 44% of SVL; lateral metatarsalia strongly connected; metatarsal tubercles poorly recognizable; no webbing between toes; relative length of toes $1 < 2 < 5 < 3 < 4$; third toe slightly longer than fifth. Skin on dorsum and ventral surface smooth.

Colour. After six years in preservative, dorsum dark grey-brown with a large, well-delimited symmetrical beige marking on each flank from the tympanic region to the groin, an inverse, brown V-shaped marking on posterior dorsum and small light brown, darkly bordered tubercle-like spots scattered on the back. Surface of head dark brown except a narrow light brown stripe between the eyes. Tympanic region dark brown bordered by a light line. Each forelimb with one distinct dark crossband, hindlimbs with several dark crossbands. The ventral side is uniformly cream. In life, the general pattern of markings and flecks is almost identical to that in preservative. Dorsum brown with cream markings and scattered irregular orange spots, well-delimited large symmetrical bright orange marking on each flank, irregular in outline, from the tympanic region to the groin. Irregular orange fleck on each heel. Dorsal surfaces of fingers and toes with a reddish tint and irregular small brown flecking. Surface of head pale brown, narrow cream stripe between the eyes. Tympanic region dark brown bordered by a cream line. Each forelimb with one distinct and one indistinct brown crossband, hindlimbs with several

brown crossbands. Cloacal region scattered with small whitish spots. Ventral surfaces fleshy white, with a bluish-violet tint on belly, throat pale brown. Iris brown with a copper tint and irregular black flecking and reticulation (Fig. 10A-B).

Variation. In comparison to the holotype, orange dorsal colour is less extensively distributed in the paratypes. In ZSM 674/2003 and 368/2004 the large irregular flecks are lacking, instead two smaller orange flecks are present dorsally in the scapular region and at level of the sacral vertebra, respectively (Fig. 10C). Another specimen (Fig. 10D) completely lacks the orange colour. The outline of darker markings on dorsum might be more or less distinctly recognizable. There seems to be also some variation concerning the dorsal skin texture in living individuals, with some individuals having almost smooth skin, others having scattered tubercles, and again others showing a finely tuberculate skin. Measurements are provided in Table 2. Several specimens of *A. emilei* show different degrees of separation of the prepollex and the first finger: for instance, in ZFMK 89185 (=ZSM 365/2004) prepollex and first finger are partly separated, whereas in ZSM 369/2004, a full separation is observed on left hand.

Etymology. We are pleased to dedicate this new species to Emile Rajeriarison, nature guide at Ranomafana National Park and one of the most knowledgeable experts of diversity and natural history of Madagascar's rainforest fauna. Emile was present during the discovery of several specimens of this new *Anodonthyla* and collected part of the type series himself.

Advertisement call. Vocalization was recorded on 18 January 2003 at 21:00 h (air temperature 20.6°C) at Ranomafana National Park (Vences *et al.*, 2006, CD 3, track 74). The advertisement call (Figs 4, 11) consists of short unpulsed, melodious notes of 58-81 ms duration, repeated in fast succession and grouped to series containing 13-14 notes ($N = 3$). Duration of these series is 2300-2580 ms ($N = 3$), resulting in a repetition rate of 5.1-5.5 notes/second within series. Intervals between these call series are irregular and may last 14.2 seconds ($N = 1$). Dominant frequency of notes is 2500-2660 Hz, additional call energy is present in a narrow frequency band at 7620-7990 Hz. There is some frequency modulation present within note series, with a slight increase in frequency from the initial to the terminal notes of a series. Although barely recognizable in our analysis, frequency modulation seems also to be present in each note, with an initial upward sweep and a short terminal drop. Compared to known calls of

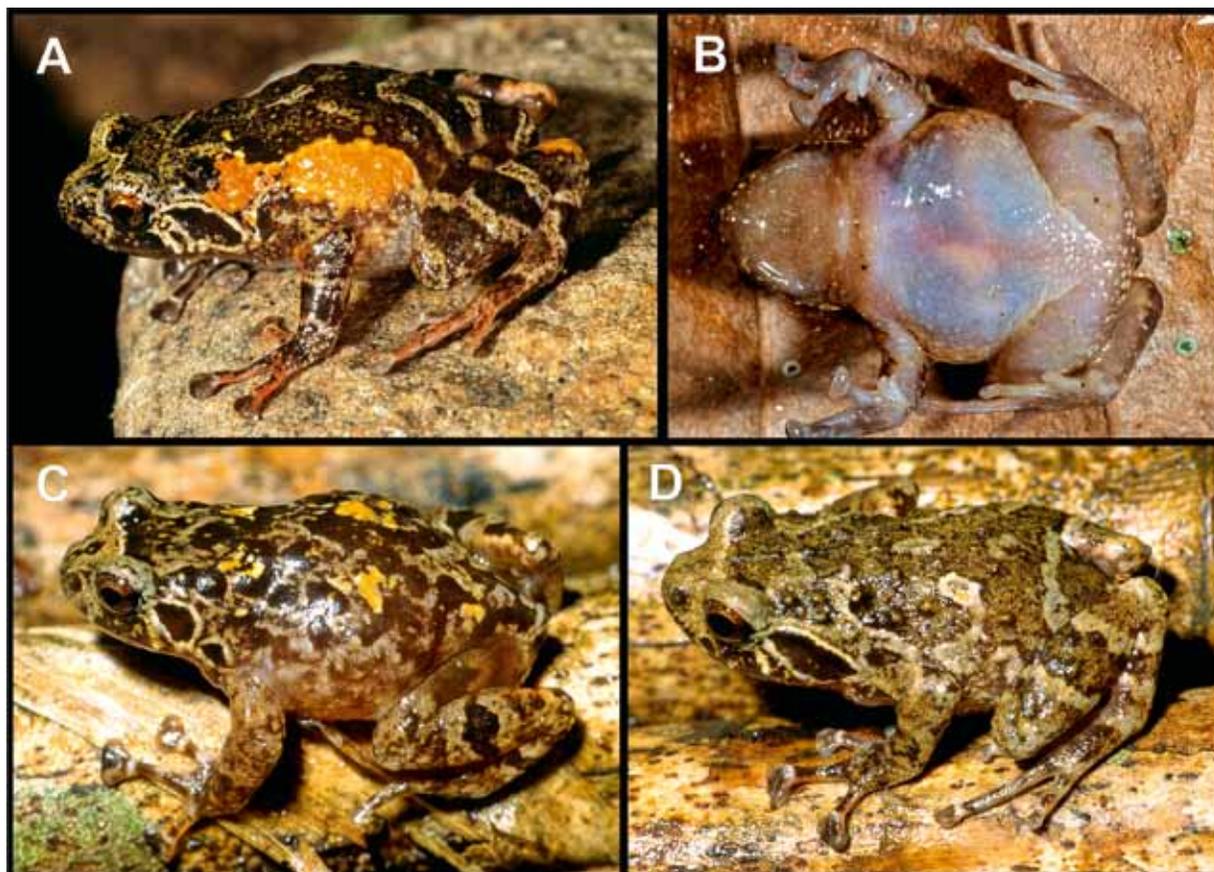


Fig. 10a-d. Specimens of *Anodonthyla emilei* in life (all males). (A-B) Holotype specimen ZSM 673/2003 from Samalaoatra (Ranomafana National Park) in dorsolateral and ventral views; (C-D) paratypes ZSM 368/2004 and 366/2004 from Maharira (Ranomafana National Park) in dorsolateral view.

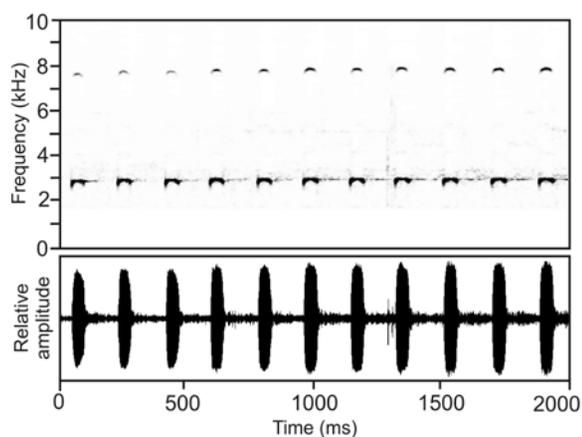


Fig. 11. Spectrogram and waveform of a part of a call series of the holotype of *Anodonthyla emilei*, recorded at Samalaoatra (Ranomafana National Park) on 18 January 2003 at an air temperature of 20.6°C.

other *Anodonthyla* species, calls of *A. emilei* are unique in being grouped to clearly defined short series, whereas calls of other species are usually very long regular continuous series, lasting up to several minutes when males are highly motivated (Glaw and Vences, 2005). Note duration in *A. emilei* is short and similar to the note duration in *A. moramora*, *A. boulengeri* and *A. nigricularis*, whereas notes of *A. theoi* and *A. vallani* are longer. The comparatively low dominant frequency in *A. emilei* calls is shared only by *A. vallani*, whereas known calls of the other species have higher dominant frequencies (Table 3).

Natural history. Calling males from *A. emilei* were found at night, calling from tree trunks 2-3 m above the ground, and in one case from inside a tree hole with a very small entrance, about 1.5 m above the ground. One specimen (ZSM 369/2004) was found together with eggs inside a tree hole.

Distribution. The species is only known from Ranomafana National Park where we found it at two

localities, Samalaotra and Maharira. Especially at Maharira the species was not rare and its characteristic calls were commonly heard, but at several other sites in and around Ranomafana we did not record the species despite intensive fieldwork.

Anodonthyla theoi sp. nov. (Fig. 12)

Holotype. ZSM 2275/2007 (field number ZCMV 5463), adult male, collected at a site in the part of Manombo Special Reserve west of the main road (coordinates not taken, but not far from our campsite at 23°01.699' S, 47°43.892' E, 44 m a.s.l.), Fianarantsoa Province, South East of Madagascar, on 24 February 2007 by M. Vences, G. Safarek, E. Rajeriarison and T. Rajofiarison.

Paratypes. ZSM 2273/2007 (ZCMV 5454), ZFMK 89186 (=ZSM 2274/2007 [ZCMV 5499]), two adult males, and UADBA uncatalogued (ZCMV 5465 and 5498), two specimens, all with same data as holotype; ZSM 2276/2007 (ZCMV 5468), one adult male, collected at a second site in Manombo Special Reserve (coordinates not taken, but ca. 1 km south of type locality), Fianarantsoa Province, on 23 February 2007 by M. Vences, G. Safarek, E. Rajeriarison and T. Rajofiarison.

Justification. This species appears to be phylogenetically related to *A. pollicaris* which however strongly differs in note repetition rate. 16S divergences of *A. theoi* are high: 3.5% to *A. pollicaris* and 7.9–11.8% to other *Anodonthyla*. Detailed analysis shows that those species with similar note repetition rates (*A. moramora* and *A. vallani* described below) differ by other call characters. This situation clearly indicates that *A. theoi* is a separate and well-defined species.

Diagnosis. A small arboreal frog assigned to *Anodonthyla* on the basis of the presence of a distinct prepollex in males. Distinguished from all other *Anodonthyla* by a significant genetic differentiation. *A. theoi* is further distinguished from *A. montana*, *A. rouxae* and *A. emilei* by smaller size (male SVL 18–20 vs. 24–34 mm), and from *A. rouxae* by the absence of distinct humeral spines in males (vs. presence). Furthermore distinguished from *A. boulengeri*, *A. pollicaris*, *A. sp. aff. boulengeri* 'Ranomafana', *A. hutchisoni*, and *A. nigrigularis* by a lower note repetition rate (0.8–0.9 vs. 1.0–3.1 per second), and from *A. moramora* by longer note duration in advertisement calls (153–230 vs. 47–80 ms). Also distinguished from *A. moramora* by larger body size (male SVL 18–20 vs. 15–17 mm) and absence of greenish shade of dorsal and ventral colour (vs. presence in many specimens in life), and from most specimens of *A. boulengeri*, *A. polli-*

caris and *A. sp. aff. boulengeri* 'Ranomafana' by a blackish vocal sac of males.

Description of holotype. Specimen in reasonably good state of preservation (muscle tissue from left thigh removed as tissue sample for molecular analysis, skin removed from right thigh, body cavity opened for parasitological study). SVL 18.9 mm (for other measurements see Table 2). Body moderately slender; head slightly wider than long, not wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protuberant, of same distance to tip of snout and to eye; canthus rostralis indistinct, concave; loreal region straight; tympanum indistinct, rounded, its diameter 48% of eye diameter; supratympanic fold indistinct; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; small maxillary teeth present; vomerine teeth absent; choanae rounded. Arms strongly thickened; subarticular tubercles poorly recognizable at the base of fingers; outer metacarpal tubercle indistinct; prepollex medium-sized and distinct, extending from the area generally occupied by the inner metacarpal tubercle to a point below digital pad of first finger; tips of first finger and prepollex diverging; fingers without webbing; relative length of fingers 1<2<4<3, inner finger rudimentary, with roundish, slightly enlarged disk, disks of fingers 2–4 distinctly enlarged, of triangular shape; keratinized nuptial pads absent, but a distinctly thickened unpigmented area on inner side of lower arm. Hindlimbs slender; tibiotarsal articulation reaching between forelimb insertion and tympanum when hindlimb adpressed along body; TL 43% of SVL; lateral metatarsalia strongly connected; metatarsal tubercles poorly recognizable; no webbing between toes; relative length of toes 1<2<5<3<4; third toe distinctly longer than fifth. Skin on dorsum and ventral surface smooth.

Colour. After two years in preservative, dorsum marbled grey and brown with small blackish dots and with oval light spots on each side of the back. Posterior head dark brown. A strong colour border between the eyes, colouration of anterior head light brown. A small black spot on each side above the tympanic region. Each forelimb with one distinct dark crossband, hindlimbs with several dark crossbands. Throat blackish, chest dark brown, belly and (remaining) ventral skin of the hindlimbs light brown, thickened ventral sides of arms unpigmented. For colour in life see Fig. 12.

Variation. Only the three male paratypes deposited in ZSM were available for comparison. They all share with the holotype the colour border between the eyes, the black spot in the tympanic region, the presence of

a distinct dark crossband on the lower arm just above the hand, and a dark throat. The dark crossbands on the hindlimbs and the contrasted dorsal pattern are much less distinct though recognizable in ZSM 2276/2007 and ZSM 2273/2007. The three paratypes have a dark W-shaped marking in the neck that is very indistinct and not clearly recognizable in the holotype. Furthermore, they share 3-4 dark spots arranged across the mid-dorsum which correspond to dermal elevations in ZFMK 89186) and lack the pair of light oval spots at middorsum which are clearly recognizable in the holotype. The arms of the paratypes are less thickened compared with the holotype.

Etymology. This species is dedicated to Theophilus ('Theo') Rajoafiarison, nature guide at Ranomafana National Park (and Emile's brother) who provided invaluable help during the collection of this new species at Manombo Special Reserve.

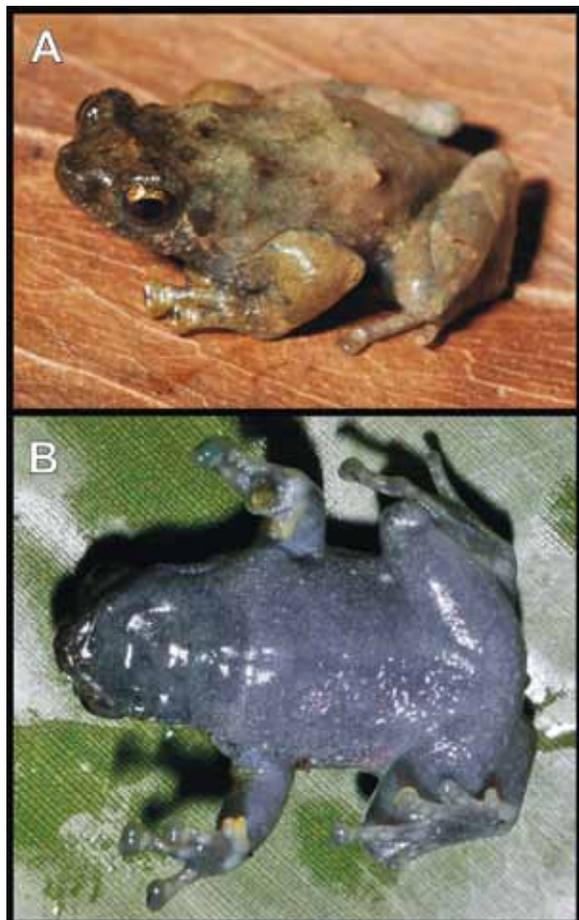


Fig. 12. Living specimen of *Anodonthyla theoi* from Manombo Special Reserve in (A) dorsolateral and (B) ventral views. Photos by Goran Safarek.

Advertisement call. Vocalization was recorded on 23 February 2007 at about 19:00 h (air temperature unknown) at Manombo, from paratype specimen ZSM 2276/2007. The advertisement call (Figs 4 and 13) consists of a moderately long note of 153-230 ms duration, repeated at regular intervals at a rate of only 0.8-0.9 notes/second. Intervals between notes range from 880-1297 ms (N = 11). If highly motivated and undisturbed, males emitted long series of notes, lasting several minutes. Notes sound melodious, but appear to be of pulsatile nature in the oscillogram, although pulses within notes are not clearly separated. Amplitude modulation within notes is obvious, with an initial increase of energy, reaching its maximum within the first third of the note's duration, subsequently dropping rapidly to a lower level. Dominant frequency of notes is 6040-6100 Hz, additional call energy is present in a narrow frequency band at approximately 9200 Hz. Compared to known calls of other *Anodonthyla* species, calls of *A. theoi* are characterized by high dominant frequency and relatively long note duration. A comparably high dominant frequency is present in calls of *A. moramora*, but note duration is shorter and repetition rate of notes is even lower compared to *A. theoi*. Similar note duration is shared by *A. vallani* and *A. theoi*, but the frequency in calls of *A. vallani* is much lower (Table 3).

Natural history. Calling males of *A. theoi* were heard at night from tree trunks, at perch heights 2-3 m above the ground.

Distribution. The species is only known from Manombo Special Reserve. Calling males in the reserve were very commonly heard.

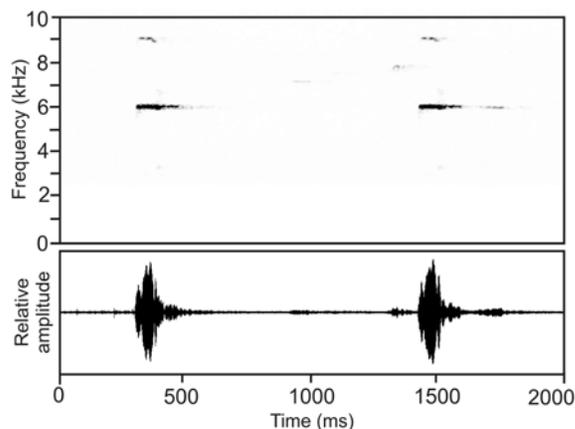


Fig. 13. Spectrogram and waveform of a part of a call series of *Anodonthyla theoi*, recorded from paratype ZSM 2276/2007 at Manombo Special Reserve on 23 February 2007.

Anodonthyla vallani sp. nov. (Fig. 14a-b)

Holotype. ZSM 86/2005 (field number FGZC 2102), adult male, collected at Ambohitantely Special Reserve, forest near camp, 0.5-1 km from: 18°11.967'S, 47°16.853'E, ca. 1580 m a.s.l., Antananarivo Province, central Madagascar, on 17 January 2005 by M. Vences, L. du Preez, P. Bora, L. Raharivololoniaina, R. D. Randrianiaina, T. Razafindraibe and E. Randriamitso.

Paratype. ZSM 87/2005 (field number FGZC 2103), adult male, same data as holotype.

Justification. This species appears to be phylogenetically related to *A. sp. aff. boulengeri* 'Ranomafana' which however strongly differs in note repetition rate and is also morphologically different. 16S divergences of *A. vallani* to all other *Anodonthyla* are very high: 9.0% to *A. sp. aff. boulengeri* 'Ranomafana' and 9.7-11.4% to other *Anodonthyla*. Detailed analysis (see below) shows that those species with similar note repetition rates (*A. theoi* and *A. moramora*) differ by other call characters. This situation clearly indicates that *A. vallani* is a separate and well-defined species. *Diagnosis*. A comparatively medium-sized arboreal frog assigned to *Anodonthyla* on the basis of the presence of a distinct prepollex in males. Distinguished from all other *Anodonthyla* by a significant genetic differentiation. *A. vallani* is further distinguished from *A. montana* by smaller size (male SVL 23-24 vs. 32-34 mm) and a less strongly developed supratympanic fold; from *A. rouxae* by the absence of distinct humeral spines in males (vs. presence) and generally by the presence of some coarse tubercles on body (vs. smooth skin). Furthermore distinguished from *A. boulengeri*, *A. pollicaris*, and *A. sp. aff. boulengeri* 'Ranomafana' by a slower note repetition rate (0.8-1.0 vs. 1.8-3.1 notes/second), and from *A. moramora* by longer note duration in advertisement calls (154-236 vs. 47-80 ms). Also distinguished from *A. boulengeri*, *A. pollicaris*, *A. sp. aff. boulengeri* 'Ranomafana', *A. moramora*, *A. theoi*, and *A. nigrigularis* by larger body size (male SVL 23-24 vs. 15-22 mm, up to 22.6 mm in one *A. boulengeri*), and from *A. moramora* by the absence of greenish shade of dorsal and ventral colour (vs. presence in many specimens in life), and from most specimens of *A. boulengeri*, *A. pollicaris* and *A. sp. aff. boulengeri* 'Ranomafana' by a blackish vocal sac of males. The calls of *A. vallani* are most similar to those of *A. theoi* in their temporal characters, but strongly differ in the dominant frequency (2850-2900 vs. 6040-6100 Hz).

Description of holotype. Specimen in excellent

state of preservation (muscle tissue from left thigh removed as tissue sample for molecular analysis). SVL 22.8 mm (for other measurements see Table 2). Body moderately slender; head wider than long, not wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protuberant, of same distance to tip of snout and to eye; canthus rostralis poorly distinct, concave; loreal region straight; tympanum indistinct, rounded, its diameter 48% of eye diameter; supratympanic fold moderately distinct; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; small maxillary teeth present; vomerine teeth absent; choanae rounded. Arms moderately thickened; subarticular tubercles recognizable at the base of fingers; outer metacarpal tubercle indistinct; prepollex medium-sized and distinct, extending from the area generally occupied by the inner metacarpal tubercle to a point below digital pad of first finger; tips of first finger and prepollex slightly diverging; fingers without webbing; relative length of fingers $1 < 2 \leq 4 < 3$, inner finger very rudimentary with roundish, slightly enlarged disk, disks of fingers 2-4 distinctly enlarged, of triangular shape; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching the tympanum when hindlimb adpressed along body; TL 47% of SVL; lateral metatarsalia strongly connected; metatarsal tubercles poorly recognizable; no webbing between toes; relative length of toes $1 < 2 < 5 < 3 < 4$; third toe distinctly longer than fifth. Skin on dorsum and ventral surface smooth.

Colour. After four years in preservative, dorsum almost uniformly dark brown with poorly recognizable dark markings and a distinct beige marking between the eyes. Head sides including tympanic region blackish. Each forelimb with one distinct dark crossband, hindlimbs with several dark crossbands. Throat blackish, chest dark brown, belly and ventral side of arms and legs brown with whitish dots. In life, dorsum dark brown with some lighter brown on posterior parts. Dorsal surfaces of arms brown, those of legs dark brown with some indistinct irregular light brown bars, posterior surfaces of thighs with irregular cream flecks. Broad cream stripe between eyes, medially extending slightly on snout, and posteriorly bordered by dark brown. Tympanic region blackish. Ventral surfaces pinkish white, covered by some violet-brown marbling, scattered with irregular small white spots, throat blackish with few scattered minute white spots. Palmar and plantar surfaces blackish brown with white tubercles. Iris bronze with some irregular black flecking.

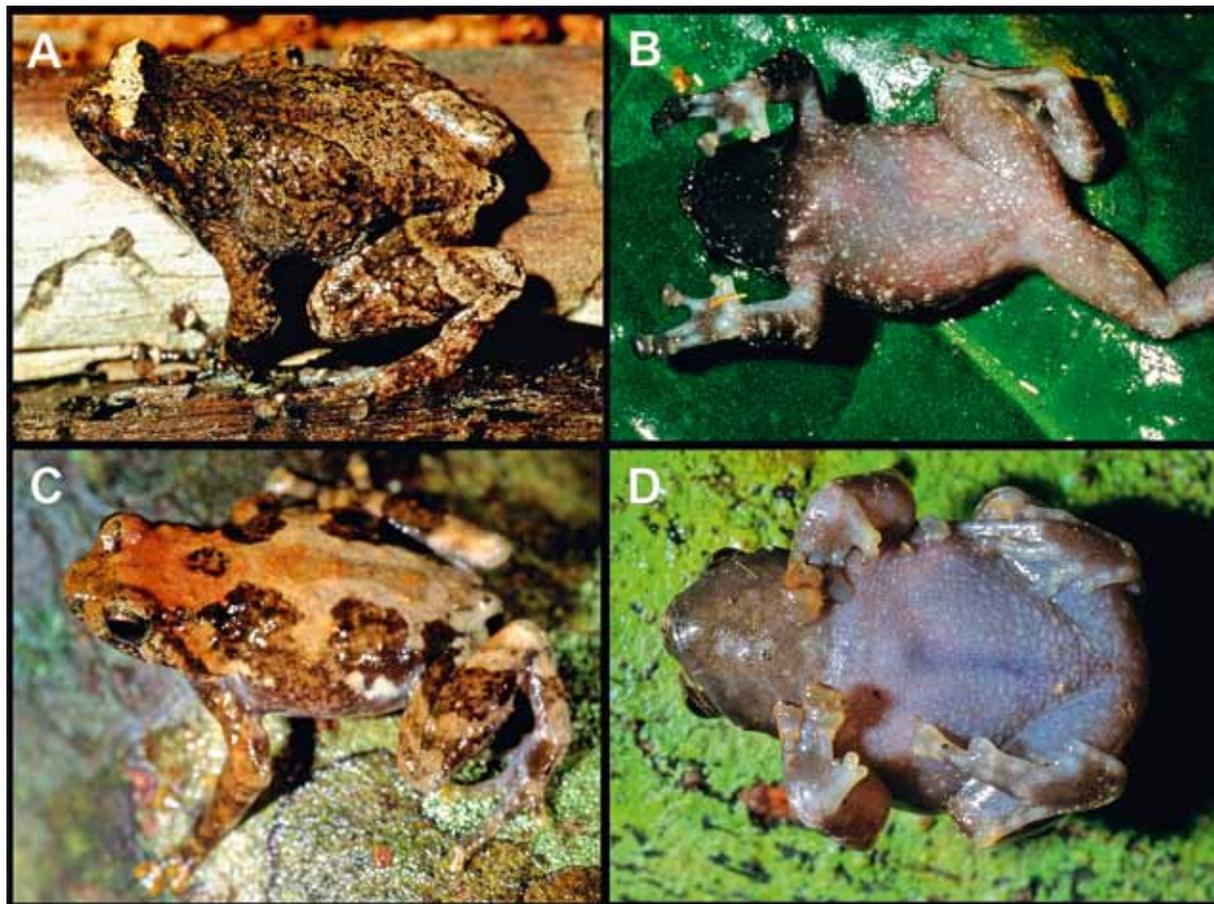


Fig. 14a-d. Specimens of *Anodonthyla vallani* and *A. nigrigularis* in life (all males). (A-B) Holotype specimen ZSM 86/2005 of *A. vallani* in dorsolateral and ventral views; (C-D) *A. nigrigularis* specimen ZSM 88/2004 from Andohahela National Park (between Isaka and Eminiminy) in dorsolateral and ventral views.

Variation. The second known specimen (paratype ZSM 87/2005) differs only very slightly from the holotype. The general colour pattern is identical, with the paratype exhibiting a slightly darker dorsum in preservative and with the pale stripe between the eyes being slightly narrower. For measurements see Table 2.

Etymology. Dedicated to our friend and colleague Denis Vallan in recognition of his pioneering work on the effects of forest fragmentation on amphibian communities at the type locality of this new species, Ambohitantely Special Reserve.

Advertisement call. Vocalization was recorded from the holotype on 17 January 2005 at about 20:00 h (air temperature unknown) at Ambohitantely Special Reserve (Vences et al., 2006, CD 3, track 73). The advertisement call (Figs 4, 15) consists of a moderately long melodious, but apparently pulsatile note of 154-236 ms

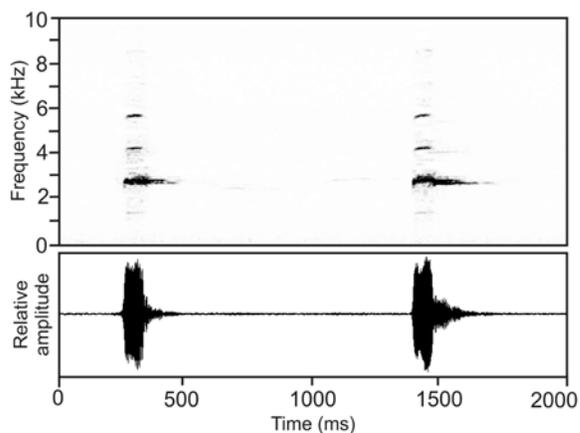


Fig. 15. Spectrogram and waveforms of a part of a call series of the holotype of *Anodonthyla vallani*, recorded at Ambohitantely Special Reserve on 17 January 2005.

duration, repeated at relatively regular intervals at a rate of only 0.8-1.0 notes/second. Intervals between notes range from 705-1016 ms (N = 14). If highly motivated and undisturbed, males emitted long series of notes, lasting several minutes. Notes exhibit some amplitude modulation, with a distinct decrease of intensity from the middle of the note towards its end. Dominant frequency of notes is 2850-2900 Hz, additional call energy is present in two frequency bands at approximately 4370 and 5800 Hz. Compared to known calls of other *Anodonthyla* species, calls of *A. vallani* are characterized by relatively long note duration, shared only with calls of *A. theoi*. Although very similar in note duration and note repetition rate, calls of the two mentioned species can easily be distinguished by frequency parameters, as the dominant frequency in *A. theoi* is 6040-6100 Hz, and thus more than double the value measured for *A. vallani*. Calls of other *Anodonthyla* species differ at least by shorter note duration (see Table 3).

Natural history. Males of *A. vallani* were observed calling at night, including nights with relatively dry weather when few other frogs were calling, from tree trunks at heights of 2-3 m.

Distribution. The species is only known from Ambohitantely Special Reserve. Calling males were very commonly heard at different sites in the reserve.

Anodonthyla jeanbai sp. nov. (Fig. 16)

Holotype. ZSM 88/2005 (field number FGZC 2405), adult male, collected at Andohahela National Park, near our campsite that was located at 24°32.642'S, 46°42.847'E, 1548 m a.s.l., Toliara Province, south-eastern Madagascar on 27 January 2005 by P. Bora, F. Glaw and M. Vences.

Paratypes. ZSM 89-96/2005 (field numbers FGZC 2406, 2407, 2409, 2411, 2414, 2416, 2418, 2419) and ZFMK 89187 (=ZSM 97/2005, field number FGZC 2421), six males and three females (see Table 2), all with same data as holotype, and UADBA uncatalogued (FGZC 2408, 2410, 2412, 2413, 2415, 2417, 2420), seven specimens, same data as holotype.

Justification. The phylogenetic tree indicates that *A. jeanbai* has a very isolated phylogenetic position, without clear relationships to any other *Anodonthyla*. Its genetic 16S divergence to other species is 9.4-12.1%. Although we have no data on the advertisement call of *A. jeanbai*, we consider this high genetic divergence in concert with various diagnostic morphological characters as given below to be clearly indicative of its species status.

Diagnosis. A small arboreal frog assigned to *Anodonthyla* on the basis of the presence of a distinct prepollex in males. Distinguished from all other *Anodonthyla* by a significant genetic differentiation. *A. jeanbai* is further distinguished from *A. montana*, *A. emilei*, *A. vallani*, and from the syntopic *A. rouxae* by smaller size (male SVL 14-20 vs. 23-34 mm), and from *A. rouxae* by the absence of distinct humeral spines in males (vs. presence). A difference visible in living *A. jeanbai* and absent from all other *Anodonthyla* is a short tuberculous fold running from directly behind the eye, slightly bent towards the center of the dorsum, and ending at the level of the forelimb insertion (sometimes continuing along the dorsum; in preserved specimens, this ridge often is only poorly recognizable). Additionally, in *A. jeanbai* the first finger is extremely reduced and in most specimens is not considerably longer than the prepollex. *A. jeanbai* is furthermore distinguished from all *Anodonthyla*, except *A. moramora*, by the presence of a yellowish pigment on ventral surfaces in life, sometimes completely extending over the venter, or just some yellow pigment on the belly; in *A. moramora*, the venter often has a greenish shade in life that could be mistaken with the yellow pigment of *A. jeanbai* whereas other species have greyish, white and black colours on the venter only. *A. jeanbai* furthermore differs by its very distinct tympanum from various other species where the tympanum is often less clearly visible, and by a comparatively long and narrow head (average ratio HW/HL 0.95, range 0.86-0.98, vs. usually >0.95 and often >1 in all other species). Also distinguished from most specimens of *A. nigrigularis*, *A. theoi* and *A. vallani* by the absence of a blackish vocal sac in males (vs. presence).

Description of holotype. Specimen in good state of preservation (muscle tissue from right thigh removed as tissue sample for molecular analysis). SVL 19.9 mm (for other measurements see Table 2). Body slender; head slightly longer than wide, not wider than body; snout slightly pointed in dorsal view, rounded in lateral views; nostrils directed laterally, slightly protuberant, of same distance to tip of snout and to eye; canthus rostralis indistinct, concave; loreal region straight; tympanum distinct, rounded, its diameter 67% of eye diameter; supratympanic fold clearly recognizable; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; small maxillary teeth poorly recognizable; vomerine teeth absent; choanae rounded. Arms moderately thickened; subarticular tubercles well recognizable at the base of



Fig. 16a-f. Specimens of *Anodonthyla jeanbai* in life, in dorsolateral and ventral views, all from Andohahela National Park. (A) Holotype specimen ZSM 88/2005; (B-F) paratype specimens, all preserved in the UADBA collection.

fingers; outer metacarpal tubercle distinct; prepollex distinct, extending from the area generally occupied by the inner metacarpal tubercle to the tip of the first finger; tips of first finger and prepollex slightly diverging; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, inner finger extremely rudimentary with roundish, rudi-

mentary disk, disks of fingers 2-4 distinctly enlarged, of triangular shape; keratinized nuptial pads absent, but a distinctly thickened unpigmented area on inner side of arm. Hindlimbs slender; tibiotarsal articulation reaching tympanum when hindlimb adpressed along body; TL 42% of SVL; lateral metatarsalia strongly connected;

►
 Fig. 17a-b. Specimens of *Anodonthyla rouxae* and *A. montana* in life in dorsolateral views. (A) Male of *A. rouxae* from Andohahela National Park (ZSM 98/2005); (B) specimen of *Anodonthyla montana* from Andringitra National Park. Arrow in A points at the humeral spine typical for *A. rouxae*.



metatarsal tubercles poorly recognizable; no webbing between toes; relative length of toes $1 < 2 < 5 < 3 < 4$; third toe distinctly longer than fifth. Skin on dorsum and ventral surface smooth.

Colour. After two years in preservative, dorsum and posterior part of head almost uniformly brown, anterior head slightly lighter brown. A thin (< 0.5 mm) light middorsal line from snout tip to cloaca. Two black spots in the inguinal region. Tympanic region light, bordered by a dark supratympanic fold. Forelimbs without distinct dark crossbands, hindlimbs with distinct dark crossbands. Cloacal region blackish. Throat, chest and ventral parts of limbs dirty yellowish with scattered brown pigment and small whitish dots; belly similarly coloured but more greyish. Thickened ventral sides of arms unpigmented.

In life, dorsum light brown with some very indistinct irregular brown flecking, pale colour covering

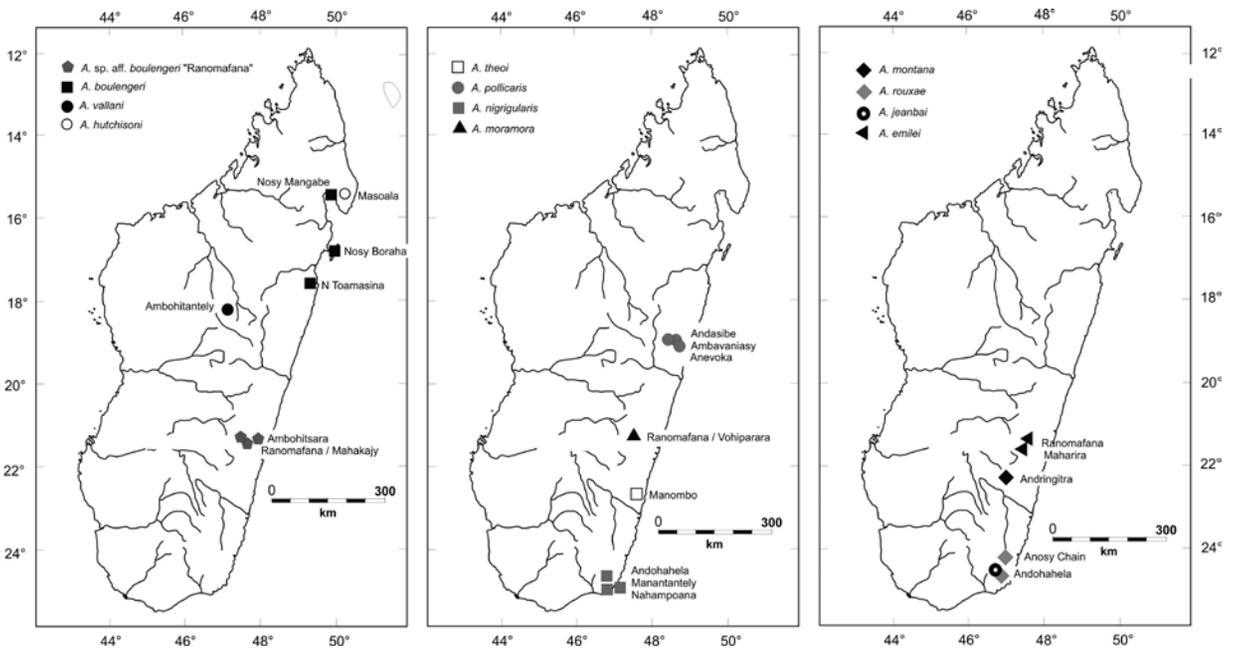


Fig. 18. Maps summarizing the reliably known distribution records of species of *Anodonthyla*. Several additional records are available for *A. bouleengeri* (e.g. Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 2007) and for *A. montana* but are not backed by bioacoustic or molecular data. Note that the positioning of the symbols on the map is approximative; especially when localities are very close to each other, symbols are partly placed slightly more away from each other to allow a better recognition.

snout and extending posteriorly to interorbital region, narrow cream vertebral line, extending from cloaca to tip of snout, black oval fleck in groin, smaller irregular black spot lateral in scapular region and on posterior dorsum. Dorsal surfaces of arms and legs light reddish brown with some indistinct irregular darker markings. Ventral colouration in life unknown. Iris bronze with fine black spotting.

Variation. *A. jeanbai* is a highly polychromatic species. As shown in Fig. 16, the colour pattern might differ considerably, with specimens exhibiting a vertebral stripe and others lacking it. Some specimens have a brown dorsal colouration with dark brown flecks encircled by thin cream lines (Fig. 16e). Many specimens exhibit a more or less regular dark ‘hourglass’ pattern in the scapular region and/or small reddish brown tubercles scattered on dorsum. Larger dark markings might be present on different dorsal body parts. However, all specimens exhibit a yellowish tint on ventral surfaces of limbs and posterior belly, and a tuberculous fold extending from the eye posteriorly to the level of insertion of forearm. Measurements are provided in Table 2.

Etymology. We dedicate this new species to the Malagasy herpetologist Jean Baptiste (Jean-Ba) Ramanamanjato who provided logistic information that proved to be crucial for the success of our expedition to the type locality, at higher elevations in Andohahela National Park.

Natural history. Specimens were found at one single site, a forest with high bamboo density at higher elevations. Specimens were very common and were found at night 1-2 m high on bamboo trunks, but no cophyline calls were heard during the single night of survey at this site. The species occurred in close syntopy with *A. rouxae* which appeared to be rarer, with only three specimens found at this site.

Distribution. The species is only known from one surveyed site at higher elevation in Andohahela National Park.

New data on other Anodonthyla species

Anodonthyla hutchisoni

This is the only species of *Anodonthyla* not included in our own collections. Fenolio *et al.* (2007) tentatively assigned a specimen from Nosy Mangabe to this species. According to our results, specimens from Nosy Mangabe however belong to *A. boulengeri*. Because on that island we have never heard calls with the slow note repetition rate apparently typical for *A. hutchisoni*, and because specimens of *A. boulengeri* from this locality are characterized by a relatively large body size as otherwise typical for *A. hutchisoni*, we conclude that so far there are no reliable records of *A. hutchisoni* from Nosy Mangabe.

Anodonthyla nigrigularis (Fig. 14c-d)

Newly recorded calls of *A. nigrigularis* from Manantantely agree with previously published recordings for the species (Table 3, Fig. 4). The same is true for an additional recording from Andohahela National Park (between Isaka and Eminiminy), recorded on 3 February 2004 (23.2°C). Despite the poor quality of this latter recording, some call parameters could be determined (not included in Table 3): dominant frequency 4400 Hz; note duration 75-90 ms, ca. 900 ms inter-note interval, repetition rate ca. 1 note/second.

Anodonthyla rouxae (Fig. 17a)

During a survey at higher elevations of Andohahela National Park we could find two males and one sub-adult specimen of this species, in an area with high density of bamboo, within primary rainforest, and syntopic with *A. jeanbai*. Both adult specimens had conspicuous humeral spines which, within *Anodonthyla*, appear to be an autapomorphy of *A. rouxae* (see also Guibé 1978). One of the collected specimens (ZSM 98/2005) had a SVL of 33.9 mm, representing the largest known male of this species.